Forest Ecology and Management 389 (2017) 249–259

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Influence of reproduction cutting methods on structure, growth and regeneration of longleaf pine forests in flatwoods and uplands

Dale G. Brockway [a,*], Kenneth W. Outcalt [b]

[a] Southern Research Station, USDA Forest Service, 521 Devall Drive, Auburn, AL 36849, United States
[b] Southern Research Station, USDA Forest Service, 320 Green Street, Athens, GA 30602, United States

ARTICLE INFO

Article history:
Received 7 September 2016
Accepted 5 January 2017

Keywords:
Pinus palustris Mill.
Continuous cover forestry
Pro-B method
Selection systems
Uneven-aged silviculture
Shelterwood methods
Even-aged silviculture

ABSTRACT

Though longleaf pine (*Pinus palustris* Mill.) forests have been primarily managed with even-aged methods, interest is increasing in uneven-aged systems, as a means of achieving a wider range of stewardship goals. Selection silviculture has been practiced on a limited scale in longleaf pine, but difficulty with using traditional approaches and absence of an evaluation across a range of site types has left managers in doubt concerning its suitability. This study was conducted to quantify the effects on stand dynamics 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. Selection treatments reduced stand basal area to ~11.5 m^2 ha^{-1} and shelterwood treatments left a basal area of ~5.8 m^2 ha^{-1}. In spite of initial decreases in tree density and standing volume, growth rates were normal in all stands (1–5% per year), as were subsequent increases in basal area and tree density. Despite the continuing abundance of saw-palmetto (*Serenoa repens* W. Bartram) cover and absence of prescribed fire during the eight post-treatment years, significant increases in pine regeneration were observed in all treated stands in the flatwoods. Because of a multi-year drought in the uplands, pine seedling numbers dramatically declined, no matter which reproduction approach was employed. Although seedling numbers eventually began to recover, they were again precipitously depressed by a wildfire in 2013. Even with such losses, sufficient pine seedlings remained in each treatment to foster successful stand regeneration. Single-tree selection produced less overall change in the forest ecosystem than group selection, which caused less alteration than shelterwood treatment. Single-tree selection appears to be an effective way for achieving stand regeneration, while maintaining a continuous canopy cover that aids in the control of woody competitors and supports an array of resource values. Selection silviculture seems to be a lower risk approach for guiding forests along a trajectory of gradual improvement, with adjustments provided by frequent surface fires and periodic tree harvest. Long-term observation will be required to verify that selection can sustain forest ecosystems on sites characterized by differing environments.

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1. Introduction

Longleaf pine (*Pinus palustris* Mill.) forests were historically one of the most extensive ecosystems in North America, spanning an estimated 37 million ha from Texas to Florida to Virginia along the southeastern Coastal Plain, Piedmont and mountains (Connor et al., 2014). However, logging, changing land use and interruption of natural fire regimes reduced longleaf pine occupancy within its natural range by 97%, to about 1 million ha (Frost, 2006). Longleaf pine forests are among the most endangered terrestrial ecosystems in the Southeastern United States (Noss et al., 1995). Despite this decline, longleaf pine ecosystems have become valued in recent times for a variety of resources of substantial ecological, economic and cultural importance. Interest among resource professionals and the public has therefore increased, concerning suitable methods for managing (and where possible restoring) longleaf pine ecosystems (Brockway et al., 2005b; Van Lear et al., 2005).

Scientific research, in recent decades, has developed 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. To these ends, the foremost goal of forest management should be applica-

* Corresponding author.
E-mail address: dbrockway@fs.fed.us (D.G. Brockway).

http://dx.doi.org/10.1016/j.foreco.2017.01.002
0378-1127/Published by Elsevier B.V.

tion of silvicultural methods that perpetuate longleaf pine ecosystems. Such methods will incorporate natural regeneration and, whenever 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 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 may be 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, 1990). Therefore, no single prescription is appropriate for managing longleaf pine forests everywhere. Prudent managers select a combination of methods appropriate for their specific environment and suitable for achieving their management goals.

Thoughtful application of timber cutting and prescribed burning is essential for creating a desirable stand structure, fostering growth of useful products, maintaining a native groundcover with high levels of biological diversity and enhancing the success of natural longleaf pine regeneration (Brockway et al., 2006; Outcalt and Brockway, 2010). In stands not dominated by herbaceous plants in the understory, precipitously reducing the forest canopy can increase woody plant competition, thereby jeopardizing longleaf pine regeneration success. Logging traffic is typically greater for shelterwood methods (more trees removed ha^{-1}) than for selection systems and this contrast may differentially influence the survival rate of young longleaf pine, as well as understory plant species (Brockway and Outcalt, 2015). No matter which stand reproduction method is implemented, frequent prescribed burning (e.g., 2 or 3-year cycle) is essential for maintaining composition, structure and function, primarily by discouraging development of competing woody plants and creating seedbed conditions favorable for regeneration and development of longleaf pine seedlings (Brockway and Lewis, 1997; Brockway and Outcalt, 2000, 2015; Outcalt, 2000, 2006; Haywood et al., 2001; Outcalt and Wade, 2004; Outcalt and Brockway, 2010).

Early studies concluded that even-aged management, with clearcutting and seed-tree methods, resulted in insufficient seed production for successful natural regeneration and needle cast to support frequent prescribed fires (Boyer and Peterson, 1983). However, the uniform shelterwood method, which typically reduces stand basal area to 6–7 $m^2\ ha^{-1}$ during the seedcut and to zero during later overwood removal, has for decades been the most widely practiced even-aged reproduction technique for naturally regenerating longleaf pine (Croker and Boyer, 1975; Boyer and White, 1990). The irregular shelterwood method, which differs from the uniform method, by foregoing complete canopy removal once a sufficient number of seedlings have become established in the understory, retains seed-bearing trees dispersed across the site and provides sufficient needle litter to support frequent surface fires. Even though the growth of longleaf pine seedlings will be slowed by competition from the mature residual pines (Boyer, 1993), the continuous canopy through time is beneficial to species dependent on such structural conditions.

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 way of achieving a broad range of 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). The group selection system most closely mimics the natural gap-phase regeneration pattern observed in longleaf pine ecosystems (Brockway and Outcalt, 1998), resulting in an uneven-aged mosaic of even-aged patches distributed across the landscape (Platt and Rathbun, 1993). Group selection creates gaps, 0.1–0.8 ha, dispersed throughout the forest matrix to simulate the desired uneven-aged structure (Brockway et al., 2006). The single-tree selection system differs from group selection, by foregoing the deliberate creation of canopy gaps when tending the forest matrix. At each cutting cycle (~10–15 years), the stand is reduced to a target basal area that is sufficiently low to initiate regeneration (11–14 $m^2\ ha^{-1}$), by harvesting across a wide range of diameter-classes, so as to approximate an exponential depletion curve for the diameter-class distribution. Long-term application of single-tree selection results in a forest with a stable uneven-aged structure and an irregular canopy with many gaps of various sizes up to 0.1 ha. In addition to blowdown from severe storms and mortality caused by localized fires and outbreaks of insects and pathogens, lightning and timber harvest are two fairly common disturbances that can augment the size of very small gaps, thus releasing suppressed longleaf pine seedlings (Outcalt, 2008). Uneven-aged systems can be useful approaches for attaining the goals of continuous cover forestry (Mason et al., 1999; Vitkova and Ni Dhubhain, 2013) and retention forestry (Franklin et al., 2007; Gustafsson et al., 2012) by implementing silviculture that emulates natural disturbance regimes, which create and maintain complex structures, natural processes and biological legacies with sufficient recovery intervals to conserve biological diversity, maintain wildlife habitat, support primary productivity and provide ecosystem services (Coates and Burton, 1997; Palik et al., 2002; Mitchell et al., 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 led to managers doubting 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, limited experience with such approaches in longleaf pine made it unclear whether selection systems could achieve productivity, habitat and biodiversity goals. 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 objective was to quantify the influence of two selection systems and two shelterwood methods on the structure, growth and regeneration of longleaf pine forests in flatwoods and uplands.

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).

Overstory vegetation was dominated by longleaf pine, with lesser amounts of slash pine. Hardwoods, primarily oaks (*Quercus* spp. L.) were infrequently present, usually as subcanopy trees. 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 (*Serenoa repens* W. Bartram) and gallberry (*Ilex glabra* (L.) A. Gray), with lesser amounts of wax myrtle (*Myrica cerifera* L.), 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 (*Aristida beyrichiana* Trin. & Rupr.), 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 this period, some planting was conducted and the residual trees were allowed to grow, as the forest slowly recovered. However, the absence of fire allowed saw-palmetto to expand and 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 and, at the beginning of this study, timber biomass estimates ranged from 56 to 193 Mg ha^{-1}. 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 (*Paspalum* spp. L.), lopsided Indiangrass (*Soghastrum secundum* (Elliott) Nash) and purpletop (*Tridens flavus* L.). The most common forbs were silverthread goldaster (*Pityopsis graminifolia* (Michx.) Nutt.), morning-glory (*Ipomea* spp. L.), milkpea (*Galactia volubilis* (L.) Britton) and noseburn (*Tragia urens* L.).

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. 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. Site records from 1993 estimated a pulpwood volume of 16.7 m^3 ha^{-1} and sawtimber volume of 31.5 m^3 ha^{-1}. 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). Frequent prescribed fires largely account for a relatively open understory that is dominated by native grasses and forbs and abundant longleaf pine seedlings.

On 29 March 2013, a wildfire which began on nearby private land burned through the study site. Although the KBDI was less than 50 units, daytime temperature 24 °C and relative humidity 56%, winds from the South varied from 5 to 24 km h^{-1} with gusts up to 34 km h^{-1} and only 40 mm of rain had fallen during the previous 30-day period, making for locally dry conditions. While char was present as high as 8 m on the bark of some overstory trees, crown scorch appeared to not exceed 33%, reflecting the resilience of mature longleaf pine trees when frequently burned with prescribed surface fire. However, forest vegetation beneath the canopy was substantially impacted.

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.

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 caused substantial windthrow damage to the eastern portion of the 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 early spring 2005, species was recorded and diameter was measured to the nearest mm for all trees greater than 2.5 cm at dbh, on subplots within each treatment plot, to establish pretreatment stand composition and structural conditions. Total height was also measured to the nearest 0.1 m for a subsample of trees representing the full range of diameter classes, to establish the height-diameter relationships for longleaf pine and slash pine. Repeated post-treatment measurements were completed following the 2006, 2007, 2008, 2010, 2012 and 2014 growing seasons to assess changes resulting from application of each stand reproduction method. During fall 2005, the number of slash pine seedlings and grass-stage (less than 15 cm tall) and bolt-stage (15 cm to 2 m tall) longleaf pine seedlings were recorded on all subplots, to establish baseline regeneration levels prior to treatment. Repeated post-treatment counts were conducted following the 2008, 2010, 2012 and 2014 growing seasons. Identification and nomenclature for species were consistent with taxonomic authorities (Clewell, 1985; Duncan and Duncan, 1988; Godfrey, 1988; Wunderlin, 1998).

2.5. Analysis

Data for trees and pine seedlings were summarized as estimates of the mean for each 9-ha plot and analyzed by treatment and change through time. Stand density and stand basal area were calculated from tree diameter data. Height-diameter relationships were computed for longleaf pine at both sites and slash pine in flatwoods through regression analysis, using height and diameter data (Hintze, 2007). Insufficient numbers of slash pine were present in uplands to develop the height-diameter relationship there for this species. The following relationships were derived for each species and site.

Longleaf pine in flatwoods:

$$H = 6.697989\ln(D) - 0.5736685 \quad R^2 = 0.467842$$

Slash pine in flatwoods:

$$H = 10.2469\ln(D) - 11.24577 \quad R^2 = 0.908599$$

Longleaf pine in uplands:

$$H = 8.864612\ln(D) - 7.610876 \quad R^2 = 0.843143$$

where
H is total tree height expressed in m
D is diameter at breast height expressed in cm

Stand volumes in $feet^3\,acre^{-1}$ were calculated, by summing individual tree volumes to a 4-inch top outside bark on a per acre basis, for each pine species at the two sites, using height and diameter data in the following equations (Saucier et al., 1981).

$$\text{Longleaf pine}: \quad V = -0.84281 + 0.00216(D^2H)$$

$$\text{Slash pine}: \quad V = -0.99865 + 0.00214(D^2H)$$

where
V is wood volume of a tree expressed in $feet^3$
H is total tree height expressed in feet
D is diameter at breast height expressed in inches

Although these equations provide output in English units, volumes were subsequently translated into metric units by using standard conversion factors.

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. Significant differences were discerned at the 0.05 level.

3. Results

3.1. Stand structure

3.1.1. Flatwoods

Harvest initially reduced stand density from 310 to 183 trees ha^{-1} with single-tree selection, 322 to 166 trees ha^{-1} with group selection, 296 to 68 trees ha^{-1} with irregular shelterwood and 293 to 55 trees ha^{-1} with uniform shelterwood (Fig. 1, Table S1). Density declines following the shelterwood seedcut (−77%, −81%) were significantly greater than those after selection harvest (−41%, −48%), with all tended stands having significantly lower densities than controls. In subsequent years (2007–2014), stand density increased to 202 trees ha^{-1} with single-tree selection, 225 trees ha^{-1} with group selection, 199 trees ha^{-1} with irregular shelterwood and 154 trees ha^{-1} with uniform shelterwood. Rates of density increase after application of the shelterwood methods (193%, 180%) were substantially greater than in stands treated with selection systems (10%, 36%).

Harvest correspondingly reduced stand basal area from 16.3 to 11.7 $m^2\,ha^{-1}$ with single-tree selection, 16.7 to 10.3 $m^2\,ha^{-1}$ with group selection, 15.8 to 4.9 $m^2\,ha^{-1}$ with irregular shelterwood and 14.3 to 4.2 $m^2\,ha^{-1}$ with uniform shelterwood (Fig. 2, Table S1). Declines in basal area after the shelterwood seedcut (−69%, −71%) were significantly greater than those following selection harvest (−28%, −38%), with all tended stands having lower residual basal areas than controls. During the next eight years, stand basal area rose to 12.8 $m^2\,ha^{-1}$ with single-tree selection, 11.9 $m^2\,ha^{-1}$ with group selection, 6.3 $m^2\,ha^{-1}$ with irregular shelterwood and 5.6 $m^2\,ha^{-1}$ with uniform shelterwood. Rates of basal area increase for shelterwood (29%, 33%) were greater than those for selection (9%, 16%).

Since selection methods harvested trees across a wide range of diameter-classes, there were no significant changes in the quadratic mean diameter of these stands (Table S1). However, shelterwood methods tended to leave larger trees in the residual overwood, thus leading to an initial increase in the mean diameter of those stands. Within six years of harvest, however, the mean diameter for shelterwood stands declined, as the number of smaller-diameter trees increased.

3.1.2. Uplands

Harvest reduced stand density from 339 to 264 trees ha^{-1} with single-tree selection, 495 to 382 trees ha^{-1} with group selection and 387 to 248 trees ha^{-1} with irregular shelterwood (Fig. 1, Table S2). After the shelterwood seedcut and single-tree selection, density was significantly lower than in controls. During the next six years, density increased to 447 trees ha^{-1} with single-tree selection, 657 trees ha^{-1} with group selection and 553 trees ha^{-1} with irregular selection. The rate of density increase for irregular shelterwood (123%) was nearly double that in selection stands (69%, 72%). By late 2014 however, density declined in all treatments (227–317 trees ha^{-1}), mortality from the 2013 wildfire.

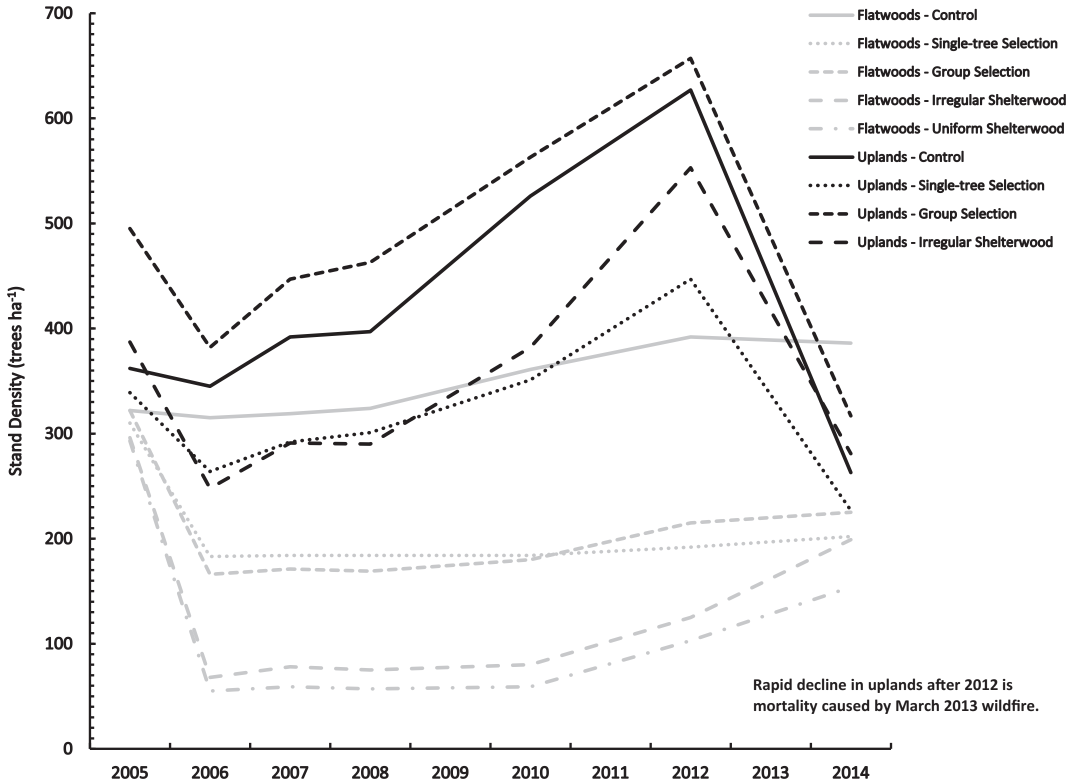

Fig. 1. Effect of reproduction cutting methods on stand density through time in flatwoods and uplands.

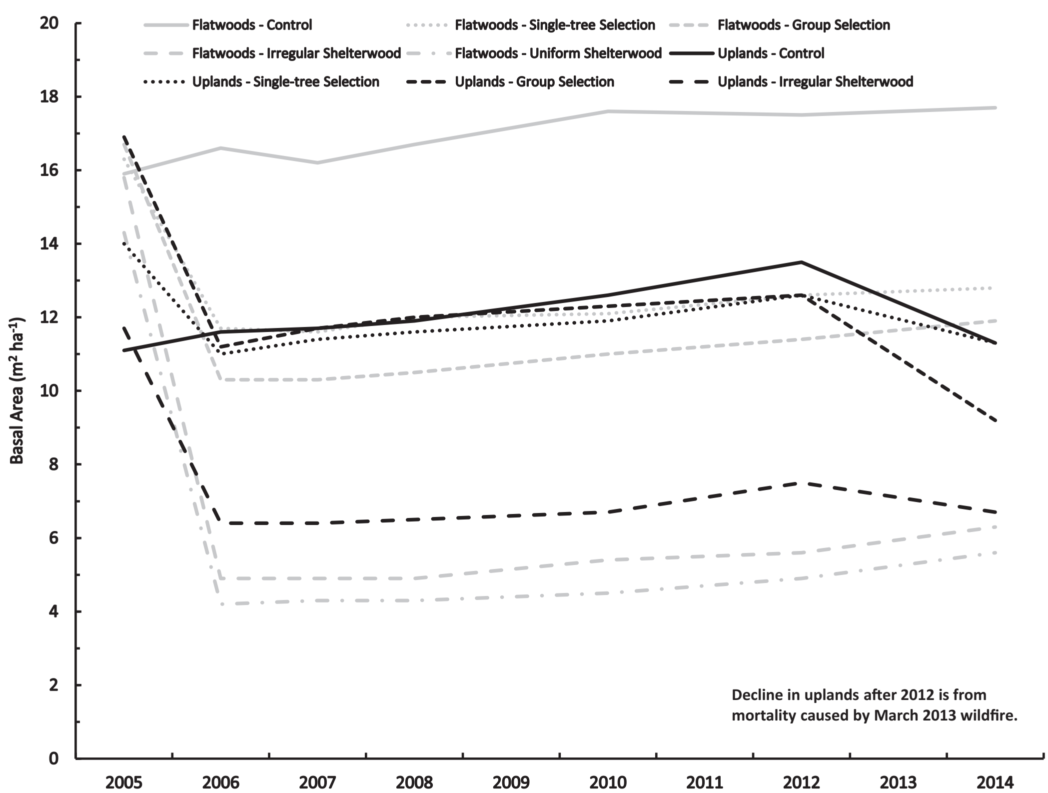

Fig. 2. Effect of reproduction cutting methods on basal area through time in flatwoods and uplands.

Harvest also reduced basal area from 14.0 to 11.0 m^2 ha^{-1} with single-tree selection, 16.9 to 11.2 m^2 ha^{-1} with group selection and 11.7 to 6.4 m^2 ha^{-1} with irregular shelterwood (Fig. 2, Table S2). The decline in basal area following the shelterwood seedcut (−45%) was greater than those following selection harvests (−21%, −34%). Only shelterwood left a basal area significantly lower than controls. Hurricane Ivan reduced basal areas from a pre-impact estimate of 17.0 m^2 ha^{-1} to the 11.1–14.0 m^2 ha^{-1} levels recorded in 2005 for control, shelterwood and single-tree selection stands, thus complicating interpretation of stand structure data. During the next six years, stand basal area rose to 12.6 m^2 ha^{-1} with single-tree selection, 12.6 m^2 ha^{-1} with group selection and 7.5 m^2 ha^{-1} with irregular shelterwood, reflecting similar rates of increase (15%, 13%, 17%). By 2014 however, wildfire mortality caused basal areas to decline to 11.3 m^2 ha^{-1} for single-tree selection, 9.2 m^2 ha^{-1} for group selection and 6.7 m^2 ha^{-1} for shelterwood (−10%, −27%, −11%).

With trees harvested across a wide range of diameter-classes, little change occurred in the average diameter of selection stands (Table S2). However, the lower quadratic mean diameter for irregular shelterwood stands resulted from removal of some large-diameter trees and, in the ensuing years, increased recruitment of smaller-diameter trees. Overstory reduction stimulated growth of numerous smaller trees, increasing the number of pines from less than 50 trees ha^{-1} to nearly 100 trees ha^{-1}, which moved into the 5-cm diameter-class. But by 2014, the mean diameter increased for all treatments, as many smaller-diameter trees were lost to wildfire.

3.2. Tree volume and growth

3.2.1. Flatwoods

Prior to harvest, total pine volume in treated stands averaged 132.6 m^3 ha^{-1}, which was not significantly different from the 135.3 m^3 ha^{-1} in controls (Table S3). These volumes were apportioned between longleaf pine and slash pine on a 76–24% basis in treated stands and 59–41% basis in controls. Prior to harvest, a significantly greater volume of longleaf pine was present only in stands scheduled for treatment with single-tree selection (121.5 m^3 ha^{-1}).

All cutting methods resulted in stand volume reductions to levels that were significantly less than volumes remaining in controls (142.5 m^3 ha^{-1}) (Fig. 3). Single-tree selection reduced stand volume to 100.7 m^3 ha^{-1} and group selection to 88.0 m^3 ha^{-1}. This greater reduction with group selection resulted from additional trees removed during harvest to create the requisite canopy gaps. Irregular shelterwood reduced stand volume to 43.6 m^3 ha^{-1} and uniform shelterwood to 36.4 m^3 ha^{-1}. Stand volume was more dramatically reduced by shelterwood methods (−68%, −69%) than by selection systems (−26%, −36%), with residual volumes in shelterwood stands significantly less than selection and controls. Though targeted for removal, slash pine was successfully reduced only by shelterwood methods. Irregular shelterwood reduced slash pine volume from 24 to 14% and uniform shelterwood from 32 to 16%.

While small volume losses occurred during the first post-treatment growing season (2007) because of minor post-harvest mortality and dry weather, by the next growing season, growth was positive at 2–4% per year. Only uniform shelterwood stands (3% per year) appeared unaffected by this early slowdown. During post-harvest years (2007–2014), cumulative volume growth increased from 100.7 to 110.3 m^3 ha^{-1} for single-tree selection (10%), 88.0 to 103.3 m^3 ha^{-1} for group selection (17%), 43.6 to 52.5 m^3 ha^{-1} for irregular shelterwood (20%) and 36.4 to 47.0 m^3 ha^{-1} for uniform shelterwood (29%), representing annual growth rates of 1.3–3.6%. During the most recent year, greatest growth rates were observed in irregular shelterwood (4%) and uniform shelterwood stands (5%). Although growth rates were 2% or less in the selection stands, these contained pine volumes twice as large as those in shelterwood stands.

3.2.2. Uplands

Total pine volume in treated stands averaged 95.7 m^3 ha^{-1} before harvest, being comparable to the 89.3 m^3 ha^{-1} in controls (Table S4). Volumes were predominantly longleaf pine, with slash pine comprising 3.5% in single-tree selection stands and 0.7% in controls. Slash pine was absent in group selection and irregular shelterwood stands.

All cutting methods resulted in stand volume reductions to levels that were significantly less than those in controls (91.4 m^3 ha^{-1}) (Fig. 3). Single-tree selection reduced volume to 72.4 m^3 ha^{-1} and group selection to 72.8 m^3 ha^{-1}. Irregular shelterwood lowered volume to 47.5 m^3 ha^{-1}, a reduction (−47%) significantly different from the two selection systems (−28%, −25%) and control. Targeted for removal, slash pine was reduced by 66% with single-tree selection.

Small volume losses (−3%) occurred with group selection and irregular shelterwood, during the first post-treatment growing season (2007), because of minor post-harvest mortality and dry weather. By the following year, volume growth was again positive (1–3% annually). Only single-tree selection stands (5% per year) were not affected by this initial slowdown. During the post-harvest years 2007–2012, cumulative volume growth increased from 72.4 to 85.3 m^3 ha^{-1} for single-tree selection (18%), 72.8 to 76.6 m^3 ha^{-1} for group selection (5%) and 47.5 to 53.0 m^3 ha^{-1} for irregular shelterwood (12%), representing annual rates of 0.8–3.0%. During 2012, the greatest growth rates were observed with irregular shelterwood (5%). While growth rates were 3% or less in selection stands, these contained greater pine volumes (52% more) than shelterwood stands. By 2014, wildfire mortality resulted in volume losses for all treatments (−2 to −13%).

3.3. Pine regeneration

3.3.1. Flatwoods

Grass-stage longleaf pine initially averaged 51 seedlings ha^{-1}, with only group selection stands significantly lower at 21 seedlings ha^{-1}. Two years post-treatment (2008), these increased 133% to an overall average of 119 seedlings ha^{-1}. In the ensuing years (2010–2014) for all cutting treatments, grass-stage numbers were significantly greater than controls (Table S5). Peak grass-stage numbers of 147 seedlings ha^{-1} for single-tree selection, 148 seedlings ha^{-1} for group selection, 221 seedlings ha^{-1} for irregular shelterwood and 155 seedlings ha^{-1} for uniform shelterwood stands were noted (Fig. 4). However, multi-year drought stress resulted in grass-stage seedling losses of −39% for single-tree selection, −29% for group selection, −20% for irregular shelterwood and −27% for uniform shelterwood stands that became evident by 2014.

Bolt-stage longleaf pine were initially present in very low densities (0–4 seedlings ha^{-1}) and increased very little during the first two post-treatment growing seasons (2007–2008). Conditions favoring increasing density of grass-stage longleaf pine had not yet sufficient time to facilitate bolting of those seedlings. By 2010, a surge in the bolt-stage appeared and a progressive increase in these numbers continued through 2014 (Fig. 5, Table S5). Peak bolt-stage numbers of 38 seedlings ha^{-1} for single-tree selection, 20 seedlings ha^{-1} for group selection, 81 seedlings ha^{-1} for irregular shelterwood and 49 seedlings ha^{-1} for uniform shelterwood were observed.

Prior to treatment, slash pine regeneration densities were low, 24–54 seedlings ha^{-1}. Greater initial densities (519 seedlings ha^{-1}) were recorded for irregular shelterwood, because one plot could not receive prescribed fire until after pre-harvest measurements. Following understory burning and overstory cutting, slash pine seedling density decreased −73% in irregular shelterwood stands, from 519 to 142 seedlings ha^{-1}. By 2008, slash pine seedling

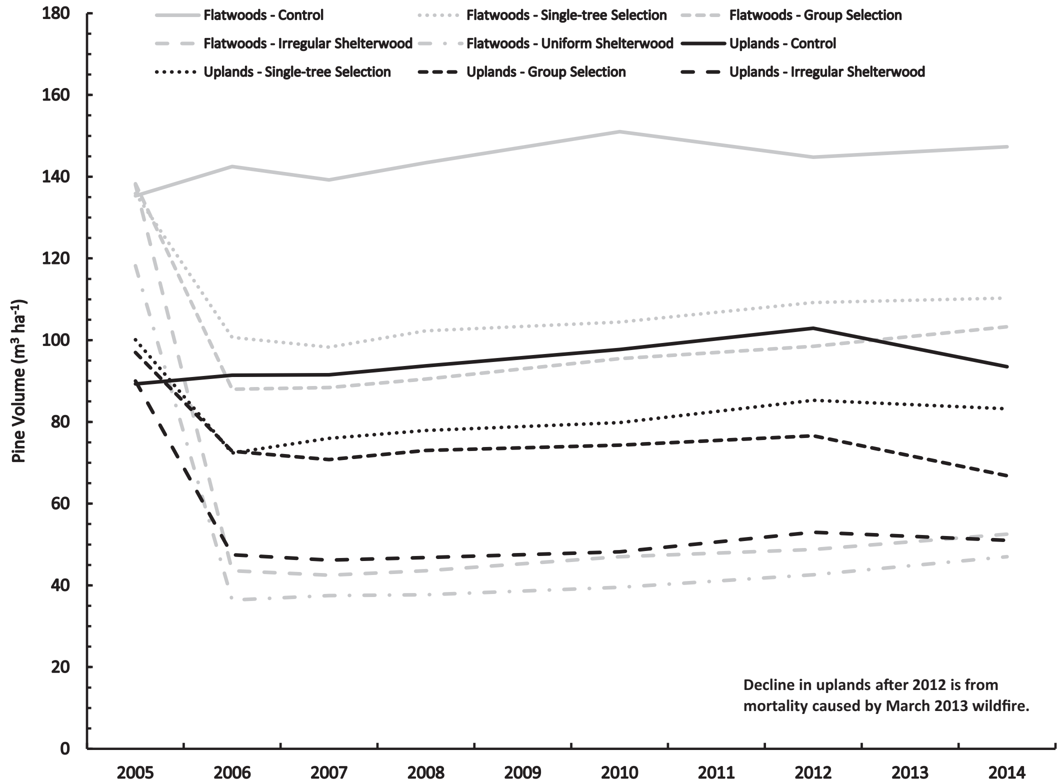

Fig. 3. Effect of reproduction cutting methods on pine volume through time in flatwoods and uplands.

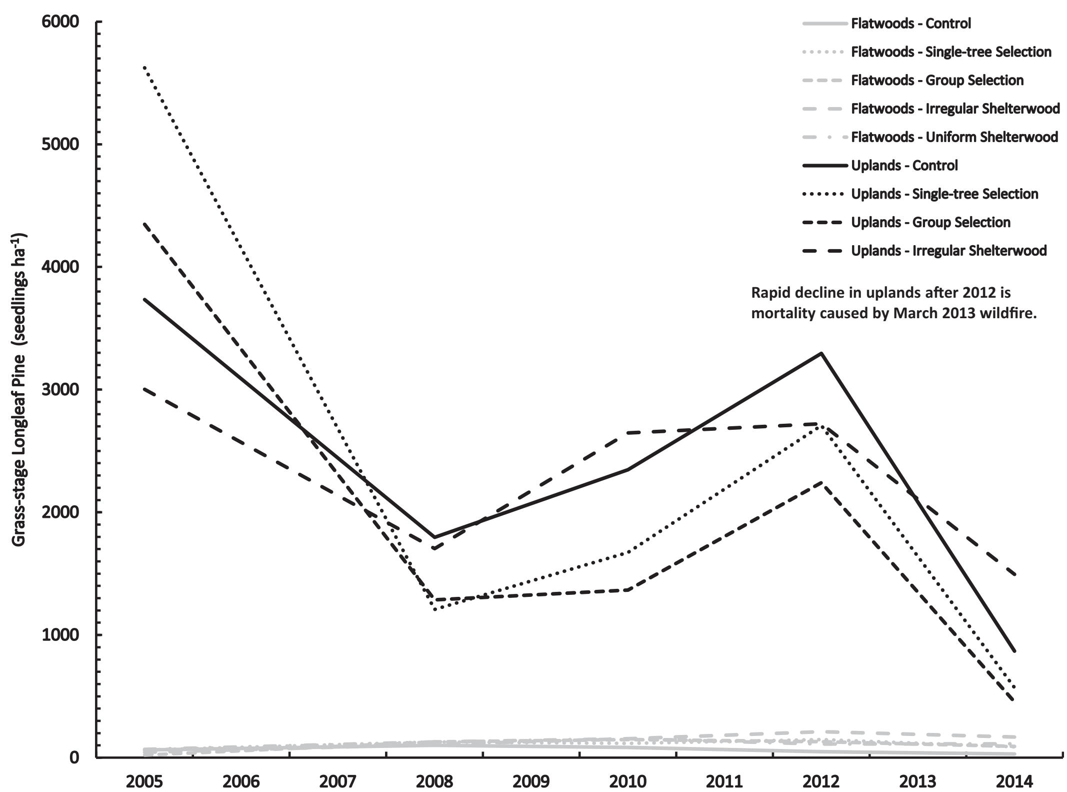

Fig. 4. Effect of reproduction cutting methods on grass-stage longleaf pine seedlings through time in flatwoods and uplands.

density increased 173% overall for other cutting treatments, from 37 to 101 seedlings ha^{-1}. During the next four years, slash pine seedling density progressively increased for all cutting treatments and remained greater than controls (Table S5). By 2012, peaks of 142 seedlings ha^{-1} for single-tree selection, 312 seedlings ha^{-1} for group selection, 295 seedlings ha^{-1} for irregular shelterwood

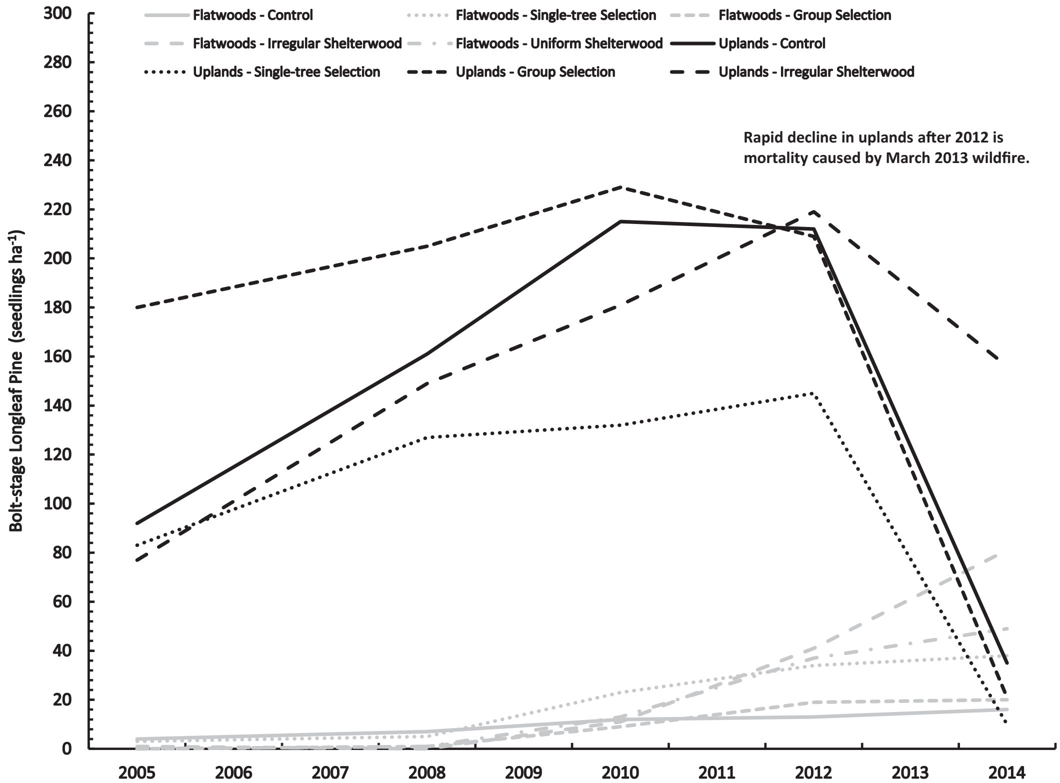

Fig. 5. Effect of reproduction cutting methods on bolt-stage longleaf pine seedlings through time in flatwoods and uplands.

and 162 seedlings ha^{-1} for uniform shelterwood were noted. But by 2014, multi-year drought stress caused losses of −8% for single-tree selection, −50% for group selection, −49% for irregular shelterwood and −18% for uniform shelterwood stands.

3.3.2. Uplands

Grass-stage longleaf pine averaged 4177 seedlings ha^{-1} before treatment, with only single-tree selection having significantly more seedlings at 5624 ha^{-1}. Two years after cutting (2008), a significant drought-related decrease (−64%) occurred, to an overall average of 1499 seedlings ha^{-1} (Fig. 4, Table S6). In following years (2010–2012), the number progressively increased to 2708 seedlings ha^{-1} for single-tree selection (124%), 2241 seedlings ha^{-1} for group selection (75%), 2721 seedlings ha^{-1} for irregular shelterwood (60%) and 3295 seedlings ha^{-1} for controls (83%). However, by 2014, grass-stage seedling losses to 571 ha^{-1} for single-tree selection (−79%), 455 ha^{-1} for group selection (−80%), 1495 ha^{-1} for irregular shelterwood (−45%) and 868 ha^{-1} for controls (−74%) could be attributed to wildfire.

Before treatment, only bolt-stage longleaf pines in group selection stands were present at significantly higher densities, 180 seedlings ha^{-1}, with those in other stands averaging 84 seedlings ha^{-1}. Two years post-harvest, except for group selection, significantly increased densities were noted for all treatments, with overall density at 160 seedlings ha^{-1} (Fig. 5, Table S6). Through time, bolt-stage numbers progressively increased to 145 seedlings ha^{-1} for single-tree selection (75%), 229 seedlings ha^{-1} for group selection (27%), 219 seedlings ha^{-1} for irregular shelterwood (184%) and 215 seedlings ha^{-1} for controls (134%). This increase in bolt-stage density was likely supported by release of grass-stage seedlings already onsite. By 2014, wildfire mortality depressed bolt-stage numbers to 10 seedlings ha^{-1} for single-tree selection (−93%), 21 seedlings ha^{-1} for group selection (−90%), 156 seedlings ha^{-1} for irregular shelterwood (−29%) and 35 seedlings ha^{-1} for controls (−83%).

Very low slash pine regeneration densities (0–23 seedlings ha^{-1}) increased after cutting in single-tree selection stands, to 127 and eventually 193 seedlings ha^{-1} (Table S6). Despite such gains, slash pine seedlings were nearly eradicated across the study site by prescribed burning during February 2010 and wildfire in 2013.

4. Discussion

4.1. Contrasting dynamics on differing sites

Stand dynamics at both sites, reflected the consequences of varying degrees of tree removal through implementation of selection systems and shelterwood methods. Results were influenced not only by the inherent characteristics of dissimilar sites, but also in flatwoods by the absence of follow-up prescribed burning because of long-term drought conditions and in uplands by application of prescribed fire during 2004, 2010 and 2011 and occurrence of a wildfire in 2013. Reductions in tree density, basal area and stand volume were anticipated, with shelterwood methods leading to greater decreases than those in selection stands. While initially low on both sites because of some post-harvest mortality, volume growth of the residual pines continued at normal rates. Although growth rates in shelterwood stands at both sites were greater than those in selection stands because of greater reduction in competition, shelterwood stands supported substantially lower pine volumes. Following prescribed burning in 2005 and timber harvest in 2006 on the flatwoods and hurricane disturbance in 2004 and timber harvest in 2006 on the uplands, all stands were stabilized and recovering, as they responded to the newly available growing space. This finding is similar to the pattern of no growth loss for periodically burned longleaf pine trees larger than sapling size (Boyer and Miller, 1994).

Subsequent to treatment, tree density, basal area and pine volume progressively increased through time on both sites. Although stand density was generally greater in the uplands than in the flatwoods, less contrast was noted between the two sites for basal area and pine volume, except for the clear disparity between controls. In uplands, tree density everywhere exceeding pretreatment levels by 2012. However, the 2013 wildfire caused decreases in tree density and basal area and increases in mean diameter, as mortality was most widespread among smaller-diameter trees. Because mortality was greatest among low-volume trees, the wildfire had proportionally less negative effect on stand volumes. Despite the negative impact of this event, we anticipate recovery and continuing growth and development of these upland stands.

Although few hardwood trees occurred in flatwoods, their presence was significant in uplands, where longleaf pine comprised only 75% of trees in these stands. This was a result of not removing hardwood trees during the 2006 harvest and earlier, when no market for hardwood forest products was available. But since they can quickly occupy growing space and vigorously compete with young longleaf pine, hardwoods should be reduced when their basal area exceeds 2.3 $m^2\,ha^{-1}$ (Boyer and White, 1990). With lower hardwood basal areas of 1.2 $m^2\,ha^{-1}$ in control stands and 1.1 $m^2\,ha^{-1}$ in irregular shelterwood stands and higher hardwood basal areas of 3.0 $m^2\,ha^{-1}$ in single-tree selection stands and 3.3 $m^2\,ha^{-1}$ in group selection stands, it would be prudent to target hardwoods for reduction during the next cutting cycle in stands tended with selection systems.

Differing management histories at these two dissimilar sites also contributed to creating contrasting understory environments for pine regeneration, with disparate trends through time. The flatwoods were in a condition typical of longleaf pine forests that had been burned little. Longleaf pine regeneration was present there at very low densities, the result of shrubs, principally saw-palmetto, which came to dominate the understory during the period of fire exclusion, prior to public acquisition (Brockway and Outcalt, 2015). With the forest floor below the widespread canopy of saw-palmetto covered by a thick mat of fallen saw-palmetto fronds and surface soil occupied by numerous large saw-palmetto rhizomes, there were few openings where pine seedlings could become established. Significantly greater numbers of longleaf pine (and slash pine) seedlings were found in stands treated with selection systems and shelterwood methods than in controls. This increase is related to forest floor disturbance from logging, decreased competition from reduced overstory densities and continuing seed production by the canopy (Brockway et al., 2006). Higher levels of logging machine traffic in shelterwood stands (i.e., about two-thirds of trees removed) reduced shrubs to a greater extent than in selection stands (i.e., about one-third of trees removed) (Brockway and Outcalt, 2015). Across substantial portions of shelterwood stands, saw-palmetto no longer dominated, but rather retreated to "islands" that were surrounded by recently-emerged swards of grass. Although pretreatment burning and mechanical disturbance from timber harvest diminished shrub dominance, so that grass-stage longleaf pine regeneration more than doubled, the number of grass-stage seedlings and slash pine seedlings declined by 2014, as the shrub canopy progressively expanded during subsequent years, when these stands could not be safely burned. While the progressive increase in bolt-stage longleaf pine among all treatments at the flatwoods was reason for optimism, such numbers were yet limited. Although these results are encouraging overall, they represent only modest progress toward obtaining effective regeneration in flatwoods, an environment which presents substantial challenges for the long-term management of longleaf pine forests (Brockway et al., 2006).

By contrast, the uplands were typical of longleaf pine forests that received periodic thinning and frequent prescribed burning, which led to a well-developed longleaf pine overstory and grass-dominated groundcover with abundant longleaf pine regeneration (Brockway et al., 2005b; Brockway and Outcalt, 2015). Although this forest was impacted by high winds in 2004, necessitating tree-salvage operations, machine traffic had little adverse influence on longleaf pine regeneration. The high levels of regeneration were a result of conditions where herbaceous plants flourished and competing shrubs and hardwoods were inhibited by frequent prescribed fire and periodic mechanical disturbance. Following harvest in 2006, grass-stage seedling numbers declined sharply across all stands, indicating this decrease was likely caused by multi-year drought stress. While grass-stage seedling numbers then steadily increased through 2012, the 2013 wildfire greatly reduced their numbers. Although grass-stage longleaf pine seedlings may persist for many years beneath the forest canopy, the longer they remain in that status, the greater the risk they will die after being weakened by drought, competition and/or fire (Boyer, 1990; Brockway and Outcalt, 1998; Brockway et al., 2006). Conversely, the post-treatment rise in bolt-stage longleaf pine in the uplands was encouraging. This increase was likely supported by the release of grass-stage seedlings that were already present. Under less stressful conditions, a greater number of grass-stage seedlings may have initiated rapid height growth and become bolt-stage longleaf pine. Competition intensity in the ambient environment can also influence the proportion of seedlings that emerge from the grass stage and enter the bolt stage (Haywood, 2000; Ramsey et al., 2003).

Results at both sites highlight the importance of fire for naturally regenerating longleaf pine. Not only is frequent prescribed burning essential for seedbed preparation, it is also crucial for discouraging the growth of woody competitors that prevent establishment, impair development and impede recruitment into the canopy (Brockway et al., 2009; Outcalt and Brockway, 2010). A strong relationship exists between fire and understory conditions in longleaf pine forests (Outcalt, 2000, 2006), with more frequently burned stands having fewer woody plants and many herbaceous species (Glitzenstein et al., 2003). While prescribed fire in flatwoods can readily curtail dominant shrubs such as gallberry (Brockway and Lewis, 1997), many burning cycles may be required to reduce a robust shrub species like saw-palmetto, with its extensive system of below-ground rhizomes and capacity for rapid regrowth. In uplands, although localized expansion of southern red oak and bluejack oak seedlings and saplings created smaller spots where competition for resources may be higher, large herbaceous-dominated areas still existed where longleaf pine seedlings could become established. Two additional cycles of prescribed fire decreased oak cover, thus discouraging these young hardwoods from ascending to the canopy and gaining dominance in the forest (Glitzenstein et al., 1995; Kush et al., 1999; Provencher et al., 2001). As highly-resilient disturbance-dependent ecosystems (Stanturf et al., 2007; Outcalt, 2008), longleaf pine forests on both sites appear well adapted to management that includes frequent cycles of prescribed surface fire and periodic partial reduction of the forest canopy through selection systems and shelterwood methods.

4.2. Impacts of reproduction techniques

Application of the two shelterwood methods in flatwoods benefitted stand dynamics by significantly reducing tree density and basal area and increasing the growing space available for regenerating pine seedlings. Since trees having the best form and growth potential were retained in the overwood as seed sources, improvement in the current growing stock was achieved and the quality of future stands was anticipated. Disturbance from logging traffic improved seedbed conditions for pine regeneration, with both longleaf pine seedlings and slash pine seedlings increasing significantly, while trees (dbh > 2.5 cm) tripled in number as stand volume steadily increased. These gains surprisingly occurred during an eight-year period when drought conditions did not allow for the application of prescribed fire in these flatwoods.

When the irregular shelterwood method was implemented in uplands, tree density and basal area were significantly reduced, also with the intention of liberating growing space to encourage pine regeneration and growth. Gains in future stand structure and performance were sought by retaining trees with desirable form and growth characteristics in the overwood. Despite a favorable change in forest structure and improvement in seedbed conditions, longleaf pine seedlings precipitously declined, as a result of drought, and then slowly increased, until a destructive wildfire again depressed grass-stage seedling numbers. Trees (dbh > 2.5 cm) increased steadily, doubling in number during the post-treatment years, until also being profoundly reduced by wildfire. Basal area and stand volume progressively improved through time and were less dramatically influenced by the wildfire, perhaps indicating that the combination of periodic harvest and frequent prescribed burning prepared larger forest trees to better withstand such disturbance (Outcalt and Wade, 2004; Outcalt, 2006; Outcalt and Brockway, 2010).

Applying the two selection systems in flatwoods reduced tree density and basal area, thus freeing growing space for pine regeneration. By retaining overstory trees with the best form and growth, as well as some older trees with broad "flat-topped" crowns for wildlife habitat, it was hoped that improvements would result in future timber production and other resource values. These systems had less impact on understory shrubs, with only group selection causing reductions in saw-palmetto that were significant, but less than those resulting from shelterwood methods (Brockway and Outcalt, 2015). This was not surprising, since logging traffic in group selection stands (removing about one-half of the mature trees) was lower than that in shelterwood stands and higher than in single-tree selection stands. Such structural change led to improved regeneration, with longleaf pine seedlings and slash pine seedlings increasing significantly in single-tree selection and group selection stands. Trees (dbh > 2.5 cm) increased in number in single-tree selection and group selection stands, as volume and basal area steadily rose through time. Without prescribed burning during the droughty eight-year post-treatment period, saw-palmetto fully recovered within six years of treatment. In the absence of fire, neither selection system disturbed these stands sufficiently to impede the long-term rise of shrubs (Brockway and Outcalt, 2015). This finding underscores the importance of frequent prescribed burning for maintaining longleaf pine forests (Brockway and Lewis, 1997; Brockway et al., 2005b; Outcalt, 2008; Outcalt and Brockway, 2010).

Implementing the two selection systems in uplands caused significant reductions in tree density and basal area, thereby enlarging the growing space available for pine regeneration. By "cutting the worst and retaining the best" trees in terms of value for wildlife habitat and timber growth, the overstory residuals were expected to provide structure and produce seed that will enhance a range of values in the future forest. Despite this favorable structural change, longleaf pine seedlings dramatically declined in single-tree selection stands and group selection stands, as a result of drought. Grass-stage seedlings and bolt-stage seedlings then progressively increased through time, until their reduction by the 2013 wildfire. Trees (dbh > 2.5 cm) also steadily increased in number, recovering to pretreatment levels by the second year after cutting, until being reduced by the wildfire. Basal area and stand volume improved through time and seemed less affected by wildfire. The 2014 increase in mean diameter indicated that wildfire-caused mortality was mostly limited to trees in smaller diameter-classes. A management regime of frequent prescribed fire plus periodic thinning created conditions that were more survivable for the larger disturbance-adapted longleaf pine trees at this site (Outcalt and Wade, 2004; Brockway et al., 2006; Outcalt, 2008; Outcalt and Brockway, 2010). Indeed, no matter which reproduction cutting method is chosen for managing longleaf pine, the importance of frequent prescribed burning should not be underestimated, if managers wish to minimize the risk of losing their forests to wildfire.

5. Conclusion

Selection systems and shelterwood methods can be beneficial treatments in longleaf pine forests, by reducing overstory canopy cover and improving the availability of light, soil resources and growing space for natural pine regeneration. The higher levels of logging machine traffic necessary for implementing shelterwood methods can be helpful in the short term, by curtailing growth of aggressively-competing woody plants, such as saw-palmetto, and preparing seedbeds for pine seedlings. However, such high levels of disturbance can also lead to adverse impacts on valued understory plants (Brockway and Outcalt, 2015) and opening the forest canopy to such high degree can, in the long term, stimulate the growth of woody competitors. By leaving a greater amount of the overstory intact, the group selection system produced less change in the forest than shelterwood methods and yet facilitated pine regeneration and continuing stand growth. The single-tree selection system caused less pronounced change in the forest than did group selection. This was not surprising, 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 regenerating longleaf pine seedlings and the understory plant community (Brockway et al., 2006). The single-tree selection system is perhaps the most cautious forest management approach, in that continuous canopy cover is maintained through time, while the overstory is harvested incrementally during numerous stand entries, which gradually free growing space for successive waves of naturally-regenerating pine. Selection also results in a high proportion of growing stock being present in sawtimber diameter-classes, thus making stands managed by such systems economically valuable, as well as supporting a broad range of resource values. 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. Given the long-term nature of forest management and the lag times often integral to natural processes, these preliminary findings should be followed-up with continuing observation.

Acknowledgements

We thank Ed Loewenstein, David Dyson, Matt Reilly, David Combs, Jeremy Waites, Ron Tucker, Erwin Chambliss, David Jones, Bryan Bulger, Eric Neiswanger, Jason O'Shell, Andy Lamborn, Chris Colburn, Mike Allen and Tom Phillips for field assistance and two anonymous reviewers for comments which improved this manuscript. Funding for this study was provided by the State of Florida, Division of Forestry [Agreement SRS-04-CO-11330123-043].

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.01.002.

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