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Factors affecting broadleaf woody vegetation in upland pine forests managed for longleaf pine restoration

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ABSTRACT

Controlling broadleaf woody plant abundance is one of the greatest challenges in longleaf pine (*Pinus palustris* Mill.) ecosystem restoration. Numerous factors have been associated with broadleaf woody plant abundance in longleaf pine ecosystems, including site quality, stand structure, and fire frequency and intensity, yet the way in which these factors vary and interact across a landscape is poorly understood. The goal of this study was to quantify the importance of environmental and management factors and their interactions on the abundance of hardwood tree and shrub species in upland pine forests managed for longleaf pine restoration in Fort Benning, GA. We measured understory, midstory, and overstory vegetation in 189 fixed-area plots, and we assembled descriptive plot data about soil texture classes, slope and aspect, and fire management history. We used classification and regression trees to model broadleaf woody species abundance. Regression trees identified fire return interval, soil texture, and slope as the most important factors affecting understory woody plant cover, with high mean cover occurring in areas with longer fire return intervals (i.e. less frequent fire), on fine-textured soils (sandy clay loams and sandy loams), and on slopes less than 6%. An interaction between soil texture and fire return interval was present and suggested that frequent fire was especially important in controlling understory broadleaf woody plants on fine-textured soils. A significant interaction emerged between soil texture and pine basal area as well, suggesting that the potential to release woody competitors with canopy removal was higher on fine-textured soils than on coarse-textured soils. The presence of hardwood stems in the midstory was most dependent upon time since burn. Other factors, such as the number of burns conducted during the growing season and topographic aspect, did not contribute significantly to variation in woody plant cover or density. Of the woody species encountered, sweetgum (*Liquidambar styraciflua* L.) was the most abundant, especially on plots with fire return intervals $\geqslant$2.6 years, on fine-textured soils, and at low pine basal areas (<9.4 m^2/ha). Other species such as persimmon (*Diospyros virginiana* L.), winged sumac (*Rhus copallinum* L.), and southern red oak (*Quercus falcata* Michx.) were commonly encountered but at low densities. Our results demonstrate the general complexity of woody species control, but more importantly indicate site differences that could be used to prioritize prescribed fire application at the landscape scale.

1. Introduction

In recent decades increasing emphasis has been placed on restoring vegetation structure and composition of longleaf pine (*Pinus palustris* Mill.) ecosystems of the southeastern United States (Van Lear et al., 2005; Walker and Silletti, 2006). Historically, longleaf pine ecosystems experienced frequent fires that maintained open stand structures and diverse, herbaceous-dominated understory vegetation communities (Frost, 2006; Peet, 2006). Twentieth-century fire exclusion resulted in the expansion of non-pine, broadleaf woody vegetation (hereafter woody vegetation), such that current conditions in many remnant longleaf pine ecosystems are characterized by abundant hardwood trees and shrubs in the understory and midstory

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vegetation strata (Van Lear et al., 2005). Once hardwoods are established, increasing fire frequency does not easily remove them because many species have the ability to resprout after aboveground stems are killed by a fire (Waldrop et al., 1992; Glitzenstein et al., 1995, 2003; Mitchell et al., 2006). Repeated cycles of topkilling and resprouting may confine woody species to the understory vegetation stratum, from which they may emerge during periods of fire suppression (Bond and Midgley, 2001; Grady and Hoffmann, 2012).

The probability of topkill from fire is generally inversely related to the size of the stem when burned (Grady and Hoffmann, 2012). On productive sites that favor rapid woody species growth, the temporal window for topkilling woody stems is shorter, requiring more frequent burning to prevent stems from developing into fire resistant sizes (Robertson and Hmielowski, 2014). While broadleaf woody vegetation is expected to be present on most sites in the longleaf pine range, species composition and woody vegetation abundance varies with edaphic conditions and site productivity, generally indexed by soil texture (Gilliam et al., 1993; Jacqmain et al., 1999; Rodgers and Provencher, 1999; Kirkman et al., 2004). More frequent fires may be needed to control woody vegetation abundance on finer textured soils compared to coarser textured soils in a given landscape. Understory vegetation responses to overstory silvicultural treatments may vary differentially with soil conditions as well (Knapp et al., 2014).

The likelihood of topkilling woody stems is contingent on characteristics of the fire regime, with high fire frequency and high fire intensity often offering the greatest woody plant control (Boyer, 1990; Robbins and Myers, 1992; Waldrop et al., 1992; Streng et al., 1993; Glitzenstein et al., 1995, 2012; Brockway and Lewis, 1997; Robertson and Hmielowski, 2014). Fire behavior and resultant effects on woody plant communities can be both complex and variable, however, based on weather conditions at the time of burning and factors such as soils and topography. Soil texture, for example, may influence fire behavior through effects on fuel types, loads, and availability. Topographic variables such as elevation, slope, and aspect also influence vegetation community composition and fuel characteristics (Gilliam et al., 1993; Peet, 2006), primarily through effects on soil moisture and light availability. For example, north-facing slopes tend to be wetter and more shaded than south-facing slopes and may enable greater fuel loads and fuel moisture. Topography also directly influences fire behavior by affecting rates of fire spread (Rothermel, 1983).

Pine canopy management activities may also interact with fire to affect the abundance of broadleaf woody vegetation. Pine overstory structure influences understory vegetation and fuels through belowground competitive effects and by mediating understory light environments (McGuire et al., 2001; Battaglia et al., 2002; Knapp et al., 2014). The removal of canopy pines via harvesting is a common restoration practice in longleaf pine ecosystems to encourage herbaceous plant community development and longleaf pine regeneration (Johnson and Gherstad, 2006; Mitchell et al., 2006). The characteristics of canopy structure (e.g., low basal area and canopy gaps) that are generally favorable for herbaceous plants and for longleaf pine seedling growth, however, are also favorable for woody plants in the sub-canopy vegetation layers (Jack et al., 2006; Pecot et al., 2007; Loudermilk et al., 2011; Knapp et al., 2014). Furthermore, the loss of pine needles as stands are thinned may reduce fuel continuity and fire intensities necessary for woody plant control (Harrington and Edwards, 1999; Jack et al., 2006; Mitchell et al., 2006; Knapp et al., 2014).

The cumulative evidence implicates multiple factors in the control of woody species abundance and structure, but how these factors interact and vary across a landscape is poorly understood. Our goal in this study was to examine the effects and interactions of multiple factors on the control of woody species abundance in a landscape managed for longleaf pine ecosystem restoration at Fort Benning, GA. Fort Benning is a 74,000 ha United States Army training installation located in west-central Georgia and eastern Alabama, where longleaf pine restoration activities have been on-going since the 1990s. The Fort Benning landscape is spatially extensive, with sites that encompass a wide range of environmental conditions, and thus provides an excellent opportunity for evaluating broad-scale patterns in woody plant dynamics. Using data from Fort Benning's long-term ecological monitoring program, we evaluated factors affecting woody plant cover in the understory vegetation stratum and woody plant density in the midstory vegetation stratum. We expected that understory woody plant cover and midstory density would be closely related to characteristics of the fire regime, such as fire return interval and time since last burn. However, we were specifically interested in better understanding how soil texture, overstory canopy conditions, and factors such as topography interact with the fire regime to affect restoration outcomes. We hypothesized that site productivity and canopy openness would each be positively related to broadleaf woody vegetation abundance, and therefore frequent fire would be especially important in controlling woody vegetation on productive, fine-textured soils as well as in stands with more open canopies. Additionally, we were interested in evaluating response patterns of individual woody species following longleaf pine restoration treatments. Such responses may be species specific based on plant tolerance to fire and life-history traits (Ratnam et al., 2011; Hoffmann et al., 2012; Veldman et al., 2013). We were particularly interested in evaluating sweetgum (*Liquidambar styraciflua* L.), as this species presents challenges to longleaf pine restoration due to its rapid growth and its potential for release following longleaf pine restoration treatments.

2. Materials and methods

2.1. Site description

Fort Benning is located in the Fall Line Sandhills region of the longleaf pine-bluestem (*Andropogon* spp; *Schizachyrium scoparium* Michx.) ecosystem described by Frost (2006). Two ecoregions are represented on Fort Benning (Keys et al., 1995). The East Gulf Coastal Plain covers approximately the northeastern two-thirds of the installation and includes the Sand Hills subsection, where soils are well-drained, loamy sands, and the major soil series are Troup and Ailey (Johnson, 1983; Green, 1997; USAIC, 2006). The Upper East Gulf Coastal Plain covers the southwestern one-third of the installation and includes the Upper Loam Hills subsection where soils are finer textured and are classified primarily as Nankin sandy loams and sandy clay loams. The topography of Fort Benning is characterized as rolling, with elevation ranging from 58 m to 226 m above sea level (USAIC, 2006). The climate is temperate, with a mean summer temperature of 26 °C and a mean winter temperature of 8 °C. Annual precipitation averages 1295 mm (USAIC, 2006). Upland sites at Fort Benning are dominated by pines and typically include a mix of longleaf, loblolly (*Pinus taeda* L.), and shortleaf (*Pinus echinata* Mill.) pines. Pine-hardwood stands are also prevalent, with common hardwood species including sweetgum, oaks (*Quercus* spp.) and hickories (*Carya* spp.). Longleaf pine is believed to have been the dominant upland species prior to Euro-American settlement of the area in the 1830s (USAIC, 2006).

In the mid-1990s, Fort Benning began an extensive longleaf pine restoration program on over 35,000 ha, with the primary objective of enhancing habitat for the federally endangered red-cockaded woodpecker (*Picoides borealis*; RCW). Fort Benning adopted at that time uneven-aged forest management practices and instituted a prescribed fire program which burns approximately 12,000 ha per year (USAIC, 2006). Longleaf pine is preferentially retained over other pine species during harvesting operations and prescribed fire is conducted with the goal of controlling woody plants and enhancing the herbaceous understory, as well as creating suitable conditions for longleaf pine seedling establishment and growth. Thinning and burning operations are aimed at gradually transitioning existing mixed pine and mixed pine-hardwood stands to longleaf pine dominance. Herbicides are used in some cases to reduce woody plant cover, but we avoided these areas in our sample in order to avoid potentially confounding effects of herbicides on woody plant dynamics.

2.2. Study design and field measurements

In 2006 Fort Benning established a long-term ecological monitoring program to evaluate changes in vegetation communities in response to longleaf pine restoration activities. A total of 189 monitoring plots (each 30 m × 30 m) were installed between 2006 and 2011. Plots were randomly located within mature (>40 years old), upland, pine-dominated stands. Overstory structure and composition were quantified by recording species and diameter at breast height (1.4 m; DBH) of each tree >10 cm DBH that occurred within each plot. Each plot was divided into four quadrats, and within each quadrat four 1 m × 1 m sub-plots were established for sub-canopy vegetation measurements ($n = 16$ sub-plots per main plot). The percent cover of understory woody vegetation (<1 m in height) was estimated visually within each sub-plot. Percent cover was recorded by vegetation functional group, including total non-pine woody vegetation, hardwood trees, shrubs, and woody vines. Cover classes were used for all percent cover estimates using the North Carolina Vegetation Survey protocol (Peet et al., 1998) as follows: 1 = trace; 2 = 0–1%; 3 = 1–2%; 4 = 2–5%; 5 = 5–10%; 6 = 10–25%; 7 = 25–50%; 8 = 50–75%; 9 = 75–95%; 10 = >95%. For the analyses, the midpoint of each cover class was used as the percent cover value. All woody stems greater than 1 m in height were tallied by species within each 1 m × 1 m plot to calculate midstory woody stem density at a scale of 16 m^2. All measurements were conducted between July and October each year, coinciding with the peak of the growing season. The slope and aspect of each monitoring plot were measured at plot center using a clinometer and a compass, respectively. Data were collected by the authors (RNA, GGS, and MLE) as well as by individuals listed in the acknowledgements section. Although plots are designed to be revisited over time to evaluate temporal change, results presented here are restricted to the initial sampling period for each plot.

2.3. Data preparation and analysis

We derived soil texture information from digitized soil classification maps (Johnson, 1983; Green, 1997) using ArcGIS (Arcmap v. 9.3; ESRI, Redlands, CA, USA). Soil textures for all plots fell into one of three texture categories: sandy clay loam, sandy loam or loamy sand. Sandy clay loams were represented by 32 plots, sandy loams by 32 plots, and loamy sands by 125 plots. We compiled fire and management histories for each plot from land management records maintained by Fort Benning's Natural Resources Management Division. We determined fire frequency from 1991 to 2011 for individual plots using a GIS fire management database depicting areas burned by year, and we calculated average fire return interval by dividing the number of times each plot burned by the number of years that had elapsed between 1991 and the year of sampling. The number of burns conducted in the growing season was determined from burn dates. Fort Benning uses March 15 as the transition date between the dormant and growing season for reporting hectares burned during the growing season to the U.S. Fish and Wildlife Service as part of its RCW habitat management program (USAIC, 2006). While we recognize that the use of a cutoff date in distinguishing between the dormant and growing season may mask year-to-year variability in climatic conditions and plant phenology important for interpreting fire effects, we elected to use this date to maintain consistency with Fort Benning's fire season characterization. Additionally, we also used a secondary cutoff date of May 15 to further distinguish burns that had been conducted in the late spring and summer. An orthorectified 1944 aerial photograph was used to determine if areas where plots are currently located were cleared or forested in 1944, as an indicator of land use history and potential legacy effects from clearing. From our plot data, we calculated stand structural characteristics, including overstory pine density (number of trees per hectare), overstory pine basal area (BA; m^2/ha), and mean overstory pine DBH per plot (cm). We transformed plot aspect to a scale of 0–2 using a cosine transformation (Beers et al., 1966) that creates high values for northerly aspects and low values for southerly aspects.

We used classification and regression tree (CART) analysis to evaluate relationships between the response variables (understory woody plant cover and midstory woody plant density) and the explanatory variables summarized in Table 1. CART is a data partitioning technique that recursively splits data into groups, with the goal of detecting natural divisions and maximizing within-group homogeneity (Breiman et al., 1984; De'ath and Fabricius, 2000). The amount of variation at each group division is described by an R^2 value, and division is halted when subsequent divisions no longer result in a gain in R^2. CART is useful for our purposes because it identifies threshold values that distinguish between groups and can therefore be used to develop decision criteria that may inform management prescriptions. We used JMP software (JMP 10.0.2, SAS Institute, Cary, NC, USA) to construct regression trees. We allowed JMP to select explanatory variables for us among the suite of independent variables included in the analysis, as opposed to pre-specifying the order in which the dependent variables are entered into the model. One of CART's primary weaknesses is a tendency to include spurious variables and over fit models (Qin and Han, 2008). We cross-validated all models to minimize over-fitting and to determine goodness of fit using JMP's k-fold cross-validation procedure with a $k = 5$. Following the CART analysis, we used general linear models (GLMs) to further

Table 1
Response and explanatory variables used in regression tree analyses. Type denotes categorical (C) versus numerical (N) and values show either categories or the ranges for the data. Fire return interval was calculated as the number of fires conducted divided by the number of elapsed years between 1991 and the year of sampling. Dates for growing season burns represent cutoff dates used to distinguish dormant from growing season burns.

	Type	Range of values
Response variable		
Understory hardwood cover	N	2.2–67.2%
Midstory hardwood density	N	0–2.75 stems/m^2
Explanatory variable		
Soil texture	C	SCL (sandy clay loam), SL (sandy loam), LS (loamy sand)
Fire return interval	N	1.5–8 years
Time since burn	N	0–3 years
Growing season burns (March 15)	N	0–9 burns
Growing season burns (May 15)	N	0–3 burns
Legacy effects	C	Forested in 1944 (0), cleared in 1944 (1)
Slope	N	0–18%
Aspect	N	0–350°
Pine density	N	22–622 trees/ha
Pine basal area	N	2.3–27.6 m^2/ha
Mean Pine DBH	N	12.5–55.5 cm

test the strength of the relationships between explanatory and response variables identified by CART, as well as to evaluate interactions suggested by the regression trees. Though we present the dominant divisions from regression tree analysis, we evaluated the full tree structures to look for embedded interactions we thought might merit additional evaluation via GLM. We used a square root transformation to normalize understory woody plant cover data within the GLMs. For the woody plant midstory density data, we used a zero-inflated Poisson regression because the data represent counts of midstory stems and contained many zeros. All GLMs were evaluated in JMP using a probability value (p-value) $\leqslant 0.05$ to evaluate significance of individual explanatory variables and their interactions.

3. Results

3.1. Understory woody plant cover

The optimal regression tree for understory woody plant cover contained 18 divisions and an overall R^2 value of 0.50 with a cross-validated R^2 of 0.38 (Fig. 1). Fire return interval formed the first and strongest division. A fire return interval of 2.7 years was identified as the division, with understory woody plant cover averaging 28.0% for fire return intervals greater than or equal to 2.7 years and 19.3% for fire return intervals less than 2.7 years. For fire return intervals greater than or equal to 2.7 years, soil texture was the next most important variable, with woody cover being greater on sandy clay loams and sandy loams (mean of 35.2%) compared to loamy sands (mean of 23.9%). On sandy clay loams and sandy loams, slope was the next most important variable for describing variation in understory woody plant cover, with an initial division at 6% slope, followed by a division at 2% slope. Understory woody cover was greater on more gentle slopes. The combination of conditions leading to the highest understory woody plant cover (mean of 50.7% for $n = 6$ plots) included slopes less than 2% on fine-textured soils such as sandy clay loams and sandy loams and where mean fire return interval since 1991 exceeded 2.7 years (Table 2).

A significant interaction between soil texture and fire return interval was suggested by CART and validated by GLM, whereby understory woody plant cover increased significantly with longer fire return intervals on sandy clay loams ($p < 0.01$, $r^2 = 0.27$) and sandy loams ($p < 0.01$, $r^2 = 0.26$) but was less sensitive on loamy sands ($p = 0.069$; Fig. 2A). An interaction between soil texture and pine basal area was also apparent further down in the regression tree (not shown in Fig. 1), whereby understory woody plant cover increased significantly with decreasing overstory pine basal area on sandy clay loams ($p < 0.001$, $r^2 = 0.49$) but did not change significantly with variation in pine basal area on sandy loams and loamy sands ($p \geqslant 0.15$; Fig. 2B). Similarly, woody cover was significantly related to slope on sandy loams ($p < 0.01$, $r^2 = 0.27$), but not on sandy clay loams or loamy sands ($p \geqslant 0.16$; Fig. 2C). Variables that were not significant predictors of understory woody plant cover included the number of growing season burns (using both March 15 and May 15 as cutoff dates), topographic aspect, and whether plots were forested or cleared in 1944.

3.2. Midstory woody stem density

Variables affecting understory woody plant cover were also important for midstory woody stem density. Regression tree analysis identified both fire and soil characteristics as important predictors of midstory woody plant density (Fig. 3). The full regression tree contained 17 divisions with an R^2 of 0.43 and a cross-validated R^2 of 0.33. The first and strongest division was related to time since burn. Midstory woody stem density increased as time since burn increased, with stem densities averaging 0.19 stems per m^2 on plots that had been burned within the previous

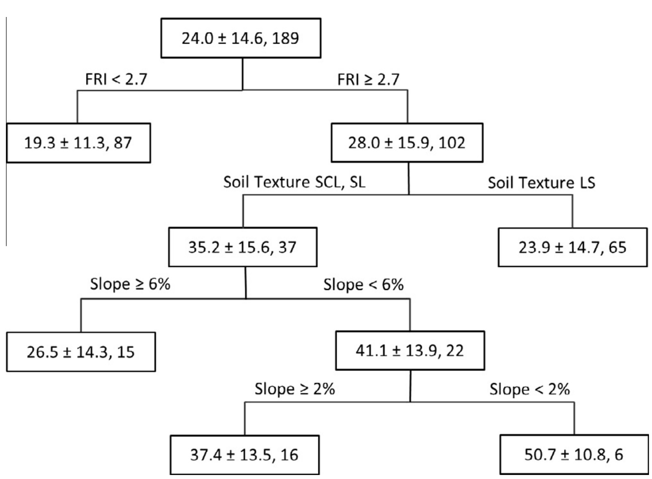

Fig. 1. Regression tree for understory broadleaf woody plant percent cover showing dominant divisions. Nodes represent estimated percent cover for each division (mean ± 1 standard deviation, number of plots). FRI stands for fire return interval. The full tree contained 18 divisions with an R^2 of 0.50 and a cross-validated R^2 of 0.38.

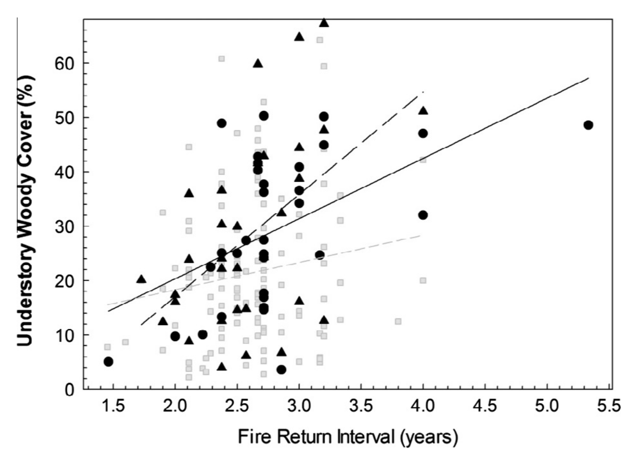

Fig. 2A. Interaction effects of soil texture and fire return interval on understory broadleaf woody plant cover. A significant positive relationship was found between fire return interval (i.e. longer return intervals) and understory woody cover ($r^2 = 0.27$, $p < 0.01$, $n = 32$) on sandy clay loams (solid line and circles) and sandy loams ($r^2 = 0.26$, $p < 0.01$, $n = 32$; long dashed line and triangles) but not on loamy sands (gray short dashed line and squares).

Table 2
Summary table from regression trees depicting response variables, groups with maximum mean values, and associated explanatory grouping variables.

Response variable	Mean (SD)	n	Explanatory variables
Understory woody cover (%)	50.7 (10.8)	6	Fire return interval $\geqslant$2.7 years, soil texture SCL/SL, slope <2%
Midstory woody density (stems per m^2)	1.27 (0.78)	13	Time since burn $\geqslant$2.0 years, soil texture SCL/SL, fire return interval $\geqslant$3.0 years
Sweetgum cover (%)	15.2 (10.7)	6	Fire return interval $\geqslant$2.6 years, soil texture SCL/SL, pine BA <9.4 m^2/ha

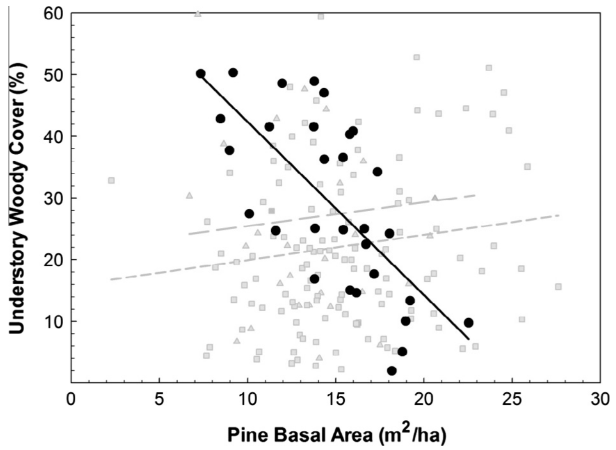

Fig. 2B. Interaction effects of soil texture and pine basal area on understory broadleaf woody plant cover. A significant negative relationship was found between pine basal area and understory woody cover ($r^2 = 0.49$, $p < 0.001$, $n = 32$) on sandy clay loams (solid line and circles) but not on sandy loams (gray long dashed line and triangles) or loamy sands (gray short dashed line and squares).

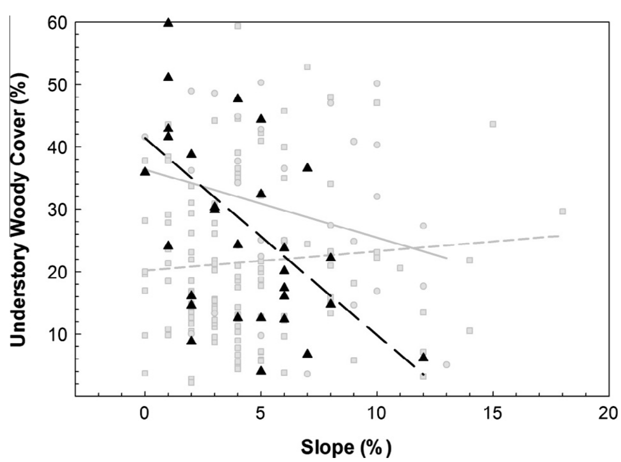

Fig. 2C. Interaction effects of soil texture and slope on understory broadleaf woody plant cover. A significant negative relationship between slope and understory woody cover was found ($r^2 = 0.27$, $p < 0.01$, $n = 32$) on sandy loams (long dashed line and triangles) but not on sandy clay loams (gray solid line and circles) or loamy sands (gray short dashed line and squares).

2 years before sampling whereas mean stem density was 0.68 stems per m^2 on plots where time since burn was greater than or equal to 2 years. Soil texture was important on sites that had not been recently burned, with greater woody stem densities on sandy clay loams and sandy loams (mean of 1.07 stems per m^2) compared to loamy sands (mean of 0.40 stems per m^2). In more recently burned sites (time since burn <2 years), greater stem densities were also associated with less frequent fire return intervals and sites with overstory pine basal areas less than 12.8 m^2 per ha. The combination of conditions leading to the highest mean midstory stem density (1.27 stems per m^2 for $n = 13$ plots) included time since burn $\geqslant$2.0 years on sandy clay loams and sandy loams, with a mean fire return interval since 1991 $\geqslant$3.0 years (Table 2).

3.3. Individual woody species

Sweetgum was the most commonly encountered woody species, occurring on over a third of the plots, and it had the highest midstory stem density, with 0.44 stems per m^2 (Fig. 4). Persimmon (*Diospyros virginiana* L.), winged sumac (*Rhus copallinum* L.), and southern red oak (*Quercus falcata* Michx.) were also commonly encountered, but their densities were typically low, averaging less than 0.20 stems per m^2. Species such as gallberry (*Ilex glabra* A. Gray) and beautyberry (*Callicarpa americana* L.) were not common but occurred in high density where they were present. Gallberry in particular appeared capable of achieving high density where it occurred, averaging 0.35 stems per m^2.

A regression tree constructed for the percent cover of sweetgum in the understory indicated the importance of frequent fire and soils (Fig. 5). The full regression tree contained 20 divisions with

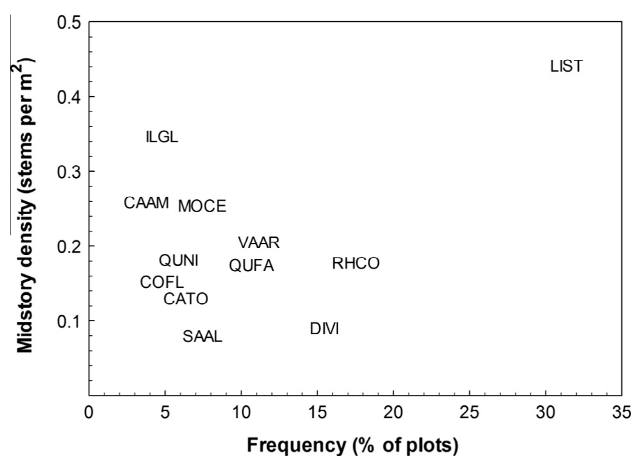

Fig. 4. Frequency (% of plots) and mean density of midstory (>1 m height) woody stems for commonly encountered woody species. Species codes: CAAM – *Callicarpa americana*, CATO – *Carya tomentosa*, COFL – *Cornus florida*, DIVI – *Diospyros virginiana*, ILGL – *Ilex glabra*, LIST – *Liquidambar styraciflua*, MOCE – *Morella cerifera*, QUFA – *Quercus falcata*, QUNI – *Quercus nigra*, RHCO – *Rhus copallinum*, SAAL – *Sassafras albidum*, VAAR – *Vaccinium arboreum*.

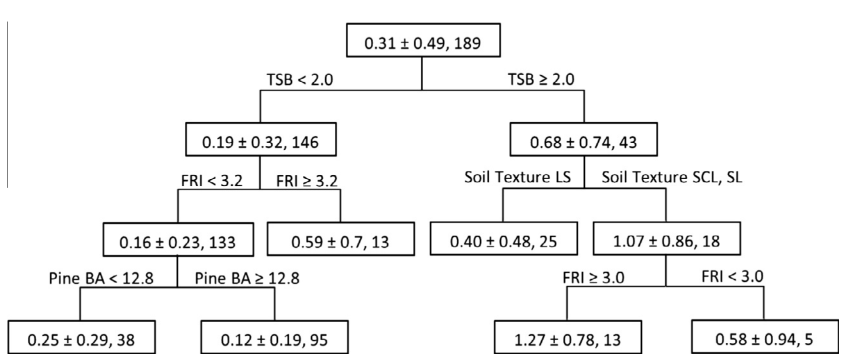

Fig. 3. Regression tree for midstory broadleaf woody plant density showing dominant divisions. Nodes represent estimated midstory density for each division (mean ± 1 standard deviation, number of plots). TSB stands for time since burn and FRI stands for fire return interval. The full tree contained 17 divisions with an R^2 of 0.43 and a cross-validated R^2 of 0.33.

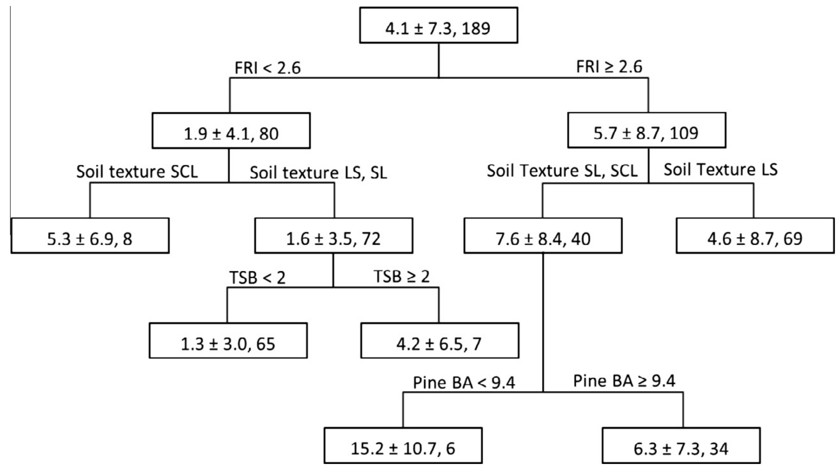

Fig. 5. Regression tree for understory sweetgum (*Liquidambar styraciflua* L.) percent cover showing dominant divisions. Nodes represent estimated percent cover for each division (mean ± 1 standard deviation, number of plots). FRI stands for fire return interval and TSB stands for time since burn. The full tree contained 20 divisions with an R^2 of 0.37 and a cross-validated R^2 of 0.18.

an overall R^2 of 0.37 and a cross-validated R^2 of 0.18. The first division was fire return interval and showed that plots with a mean fire return interval greater than or equal to 2.6 years had greater sweetgum cover compared to more frequently burned plots. On plots with fire return intervals equal to or exceeding 2.6 years, sweetgum cover averaged 7.6% on sandy clay loams and sandy loams compared to 4.6% on loamy sands. Soil texture was important on more frequently burned plots, with sweetgum cover averaging 5.3% on sandy clay loams compared to 1.6% on sandy loams and loamy sands. Time since burn and overstory pine basal area were also identified as important but less prominent contributors. The combination of conditions leading to the greatest understory sweetgum cover (mean of 15.2% for $n = 6$ plots) included areas where the mean fire return interval since 1991 was equal to or exceeded 2.6 years, on sandy clay loams and sandy loams, and where overstory pine basal area was less than 9.4 m^2 per ha (Table 2).

4. Discussion

Managing for desirable vegetation structure and composition is important to restoration in longleaf pine ecosystems and often involves management activities aimed at enhancing herbaceous ground layer vegetation and limiting the cover and abundance of broadleaf woody vegetation (Brockway et al., 2005; Van Lear et al., 2005). Our results emphasize the importance of considering multiple factors and their potential interactions when planning for woody vegetation control during longleaf pine ecosystem restoration. The importance of fire was highlighted by our analyses, similar to numerous other studies demonstrating the effectiveness of fire in controlling the distribution of woody plants in longleaf pine ecosystems (Boyer, 1990; Robbins and Myers, 1992; Waldrop et al., 1992; Streng et al., 1993; Glitzenstein et al., 1995, 2012; Brockway and Lewis, 1997; Loudermilk et al., 2011). Fire frequency was clearly important in our study, with both woody plant cover and midstory stem densities reduced on sites that experienced frequent burning. Our results indicated that a fire return interval of 2–3 years is important in reducing understory woody plant cover, especially on fine-textured soils where recovery of woody plants may occur relatively quickly. Our results are similar to other studies citing a 1–3 year fire return interval as being necessary for limiting woody plant abundance (Waldrop et al., 1992; Glitzenstein et al., 2012). That frequent fire did not completely eliminate woody vegetation was not unexpected, as many woody species within longleaf pine ecosystems are capable of post-fire resprouting and often quickly regain their pre-fire stature (Boyer, 1990; Loudermilk et al., 2011; Grady and Hoffmann, 2012; Hiers et al., 2014; Robertson and Hmielowski, 2014). While many individual hardwoods can effectively get caught in a "fire trap," repeatedly resprouting after being topkilled, some may eventually escape into the midstory and canopy owing to various factors such as canopy disturbance (e.g. wind throws) as well as spatial and temporal variability among fires. Thus woody plant growth into the midstory could be influenced by mean fire interval and time since burn, as shown by our results.

While fire frequency was important in our study, we did not find an effect of fire season on woody vegetation. The current literature with regard to dormant versus growing-season burning is mixed, with some studies finding that growing season burns are more effective in controlling woody plant abundance than dormant season burns (Boyer, 1990; Robbins and Myers, 1992; Streng et al., 1993; Glitzenstein et al., 1995; Robertson and Hmielowski, 2014) and other studies finding no effect of fire season (Boyer, 1995; Kush et al., 1999; Glitzenstein et al., 2008). In one long-term study, Waldrop et al. (1992) found that annual summer burning nearly eliminated woody stems, sprouts, and root stocks, whereas annual dormant season burning was not as effective in reducing woody stem densities. The effectiveness of growing season burns may be due to a number of factors, including the increased likelihood of having high-intensity fires during spring and summer and the physiologically vulnerable state of woody plants during the growing season (Boyer, 1993; Glitzenstein et al., 1995; Drewa et al., 2002). Failure to detect a significant influence of growing season burning in our study may be due to the observational nature of our dataset and an inability to adequately separate the effects of fire frequency and fire season in our analysis. Studies like ours, however, that do not find an effect of fire seasonality on woody plant dynamics often point to the importance of fire intensity rather than season in explaining fire effects (Boyer, 1995; Kush et al., 1999). Dormant season burning can be as intense as growing season burning, depending on fuel and weather conditions at the time of burn (Glitzenstein et al., 1995; Knapp et al., 2009). In addition, resprouting ability may be species-specific and therefore fire seasonality may not affect all woody species in the same way (Robbins and Myers, 1992). Many previous studies have focused on oaks, whereas sweetgum, a prolific resprouter following topkill by fire (Coladonato, 1992), was the dominant species in our sample. Overall, our study is consistent with other studies which suggest that the importance of fire frequency outweighs the importance of season of burning for managing vegetation structure in longleaf pine ecosystems (Glitzenstein et al., 2008).

Both understory cover and midstory density were affected most strongly by some fire measure, either time since the last burn or mean fire return interval. However, soil texture also exerted a strong influence on hardwood abundance, especially with lengthening fire return intervals. In both the understory and midstory vegetation strata, hardwood abundance was greater on fine-textured soils (sandy clay loams and sandy loams) compared to coarse-textured loamy sands. Fine-textured soils typically exhibit higher water holding capacity, higher moisture status, and higher native fertility compared to coarse-textured soils, which together result in overall higher site quality and productivity and may create optimal conditions for hardwood growth (Aber and Mellilo, 1991; Brockway et al., 2005). More rapid growth on favorable sites increases the likelihood of survival to a size that permits escape into the midstory. Our results indicate that frequent burning to restrict or decrease hardwood abundance in longleaf pine stands will be more important on fine-textured than in better drained sandy soils where slower growth allows a longer fire-free window without losing hardwoods to larger size classes where they may be more fire resistant.

Slope emerged as another important variable in our analysis, with greater understory woody plant cover associated with gentle slopes, generally less than 6%. The relationship between slope and woody plant cover may be related to the effect of slope on soil characteristics. Flat terrain is often characterized by deeper soils and greater soil volumes, which may enable higher soil moisture and nutrient availability. Steeper slopes, on the other hand, may be characterized by shallower, drier soils due to erosional processes (Jenny, 1994). We also found an interaction between slope and soil texture, such that the effects of slope on understory woody plant cover were more pronounced on fine-textured soils compared to coarse-textured soils. These results suggest that woody plant proliferation may occur more readily on flat terrain on fine-textured soils compared to similar terrain on coarse-textured soils. In addition to soils, there may be an interaction between slope and fire behavior that influences woody plant dynamics. The effect of slope on fire behavior is difficult to parse out in our analysis, however, as we do not have information that distinguishes upslope head fires from downslope backing fires. Upslope head fires are typically characterized by increased rates of spread and higher flame lengths (Rothermel, 1983), which may be more likely to topkill hardwood stems. Downslope backing fires, on the other hand, are characterized by slower rates of spread and lower flame lengths but longer residence times. Interactions among slope and fire behavior are likely highly heterogenous across the Fort Benning landscape based on fuels, weather, and other factors affecting fire behavior such as ignition patterns, but may provide an avenue for future research to inform tactical approaches in the use of prescribed fire to manage woody plants.

Canopy thinning is often used as a restoration practice to reduce overstory competition with the herbaceous understory and to promote longleaf pine regeneration (Harrington and Edwards, 1999; Johnson and Gherstad, 2006; Mitchell et al., 2006; Knapp et al., 2014), but thinning can also have undesirable effects on woody vegetation and fire management. For example, Harrington and Edwards (1999) documented a doubling of shrub and woody vine cover as stands were thinned from 1440 to 635 pines per ha, while Jack et al. (2006) described a threefold increase in woody biomass within canopy gaps cut to encourage longleaf pine regeneration. In our study, we found a relationship between overstory pine basal area and understory woody plant cover but only on fine-textured soils. We expect that the higher productivity of the fine-textured soils resulted in rapid growth of woody plants following release from canopy competition. Maintaining higher basal areas and spatially distributing residual trees in ways that ensure relatively continuous needle cast for fire management are both important considerations for restoration, especially on fine-textured soils (Palik et al., 1997; Kirkman et al., 2007; Hu et al., 2012; Knapp et al., 2014).

While broadleaf woody vegetation management is an important aspect of longleaf pine ecosystem restoration, it is also important to note that some degree of woody plant cover is appropriate and desirable within longleaf pine ecosystems. Results from a reference community study on Fort Benning suggest that high quality longleaf pine sites are characterized by 0–15% understory hardwood and shrub cover (Mulligan and Hermann, 2004). Consideration of woody species composition is important here as well. Deciduous oaks, for example, are a natural component of longleaf pine ecosystems and provide numerous benefits to wildlife (Greenberg and Simons, 1999; Perkins et al., 2008; Hiers et al., 2014). Other woody species such as sweetgum, however, are capable of rapidly overtaking sites and outcompeting desirable herbaceous species and longleaf pine regeneration. Sweetgum is more common across the upland landscape at Fort Benning now than it was historically. Using witness tree data from survey plats associated with the Georgia Land Lottery of 1827, Frost and Langley (2009) estimated that sweetgum made up 0.6% of all trees recorded historically, whereas 37% of plots surveyed by Frost and Langley (2009) currently contained sweetgum. Although sweetgum resprouts prolifically following topkill by fire, it is considered a fire-sensitive species that was historically found primarily in bottomlands, on slopes, and in upland fire refugia, but it has spread widely throughout the southeastern United States following 20th century fire exclusion (Coladonato, 1992; Surrette et al., 2008; Frost and Langley, 2009). Traits such as thin bark and a relatively high growth rate suggest that sweetgum is a forest species typically restricted from frequently burned pine woodlands and savannas but that invades with fire exclusion (Ratnam et al., 2011; Hoffmann et al., 2012; Veldman et al., 2013). In our study, high sweetgum cover was associated with less frequent fire, fine-textured soils, and low overstory basal areas ($<9.4\ m^2/ha$). Our results suggest that managers should be aware of the release potential of sweetgum under these conditions in particular, and that treatment of sweetgum may be required prior to other longleaf pine restoration treatments, such as canopy thinning, to avoid the loss of sites to this aggressive species. Control of sweetgum, particularly on productive sites, may require more extreme fire management or treatments such as herbicides. In contrast, species such as persimmon, though common, do not seem to pose as great a threat in terms of aggressive proliferation, especially in frequently burned stands.

While our study points to several important factors that influence broadleaf woody vegetation, our best model explained only 50% of the variation in understory woody plant cover. The lack of a strong model fit further highlights the complexity of woody plant dynamics in longleaf pine ecosystems and may point to the importance of additional factors such as land-use history that we were unable to account for adequately in our analyses. Current understory woody cover and midstory stem density were not related to whether plots were forested in 1944 in our analyses, though this measure of land-use history is coarse and does not account for land uses such as agriculture, which has been shown to be important in explaining present-day species composition and structure within longleaf pine ecosystems (Brudvig and Damschen, 2011). Prior to its establishment as a United States Army training installation in 1918, Fort Benning was farmed primarily for cotton (USAIC, 2006). Land use legacies undoubtedly affect present-day vegetation structure and composition and set the stage for current day restoration activities (Frost, 2006). While it is difficult to explicitly account for legacies of past land uses when planning for restoration, having some understanding of both the environment and history of individual sites is important in anticipating restoration trajectories and effects of restoration treatments on vegetation structure and composition.

5. Conclusions and management recommendations

Starting conditions for restoration of longleaf pine ecosystems often include abundant broadleaved woody vegetation in the understory and midstory strata due to fire exclusion and other practices that have enabled woody plants to establish and proliferate. Restoration treatments aimed at enhancing understory herbaceous vegetation and longleaf pine regeneration may also create suitable conditions for the establishment and growth of woody competitors. It is important to consider the effects of multiple abiotic and biotic factors and their interactive influence on woody vegetation when prescribing longleaf pine restoration treatments. Our analysis is unique in that it identified specific thresholds in woody plant abundance related to fire return intervals, overstory pine basal area, and variability with site conditions that may directly inform management prescriptions. For example, our results point to the importance of frequent prescribed fire (2–3 year return interval) in controlling woody vegetation, but also suggest that soil texture is important, particularly in mediating the response of woody plants to fire and overstory canopy removal. On fine-textured soils such as sandy clay loams and sandy loams, we recommend that canopy treatments be designed in a way that maintains fine fuel continuity for enhancing fire management, particularly if woody vegetation is abundant in the understory and midstory vegetation strata prior to treatment. Treatments designed to control sweetgum should precede canopy removal, due to the species' fast growth, prolific vegetative regeneration, and high potential for release. Similar recommendations apply to sites with coarse-textured soils, such as loamy sands, although managers may have more flexibility in fire management and in creating diverse stand structures due to less potential for woody plant release. Frequent fire, however, is important in all cases and across all soil conditions in order to effectively control understory and midstory woody plants and meet longleaf pine ecosystem restoration objectives for vegetation structure and composition.

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