United States
Department of
Agriculture

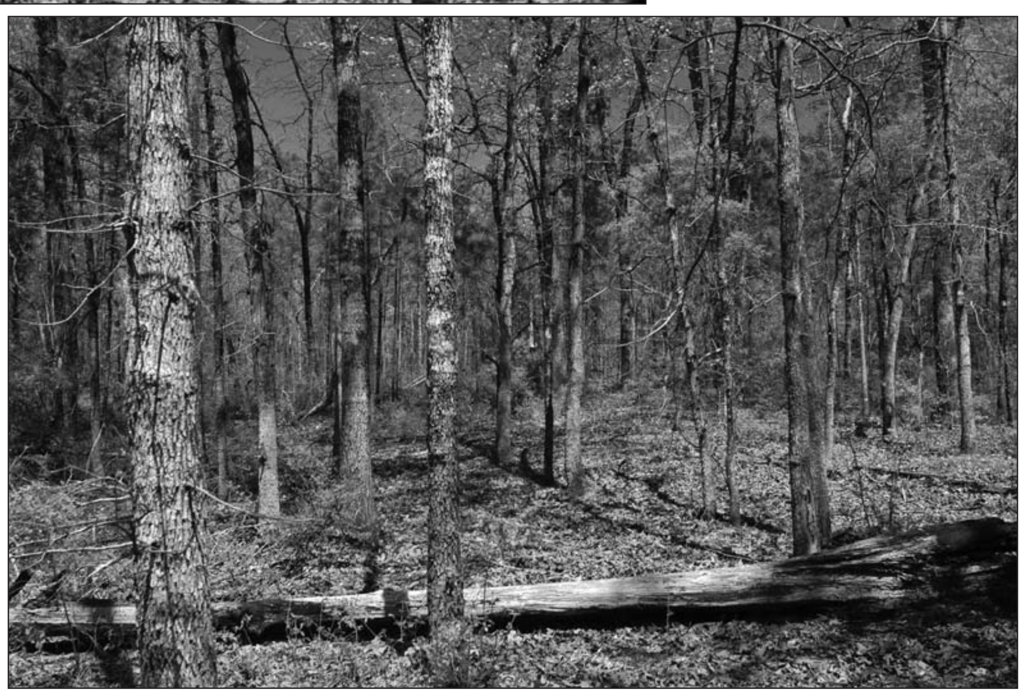
Forest Service

**Southern
Research Station**

General Technical
Report SRS-129

Disturbance from Southern Pine Beetle, Suppression, and Wildfire Affects Vegetation Composition in Central Louisiana: A Case Study

**T.W. Coleman, Alton Martin, Jr., J.R. Meeker,
S.R. Clarke, and L.K. Rieske**



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Cover photos: Kisatchie Hills Wilderness Area imaged 2 years post-disturbance (1989) on the top, and same perspective 16 years post-disturbance (2003), below. Courtesy of Alton Martin Jr. (top) and Eric Vallery (bottom).

August 2010

Southern Research Station
200 W.T. Weaver Blvd.
Asheville, NC 28804

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Abstract

We assessed plant composition and forest succession following tree mortality from infestation of southern pine beetle *(Dendroctonus frontalis),* associated suppression, and wildfire in two forest types, pine (*Pinus* spp.) with mixed hardwood and longleaf pine *(P. palustris*). In this case study, vegetation was assessed in 2003 using methodology and experimental framework established 16 years earlier. We examined changes in vegetation composition from the 1980s to 2003 in each forest stand type and used the Forest Vegetation Simulator to predict forest succession.

In the pine-hardwood stand, total plant and woody plant abundance and richness increased over the study while total plant evenness decreased. The Forest Vegetation Simulator predicts the pine-mixed hardwood will shift to loblolly pine-hardwood after 50 years. In the longleaf pine stand, total plant abundance and richness increased. The interacting disturbances enhanced forb, shrub, and tree abundance. Forb and shrub species richness also increased. Modeling predicts the longleaf pine stand will shift to loblolly pine *(P. taeda)* following the disturbance events. Although stand predictions are different for each initial forest type, predicted pine and hardwood basal area represent high susceptibility to future SPB outbreaks.

The interaction of these three disturbance events (beetle infestation, associated suppression, and wildfire) appears to maintain pine composition, but also the potential for additional SPB-caused mortality, though thinning may reduce the susceptibility of these stands to bark beetle disturbance. The unique opportunity to assess interacting disturbances and natural succession was the motivation for our study, but our inferences are limited due to constraints of the experimental design.

Keywords: Cut-and-leave suppression, Forest Vegetation Simulator, loblolly pine, southern pine beetle, wildfire.

Introduction

Forest disturbances, such as insect outbreaks or fire, alter species composition and potentially influence forest succession (Sousa 1984). Bark beetles are a major threat to forests worldwide, and in recent years an estimated 50 species of exotic bark beetles have established in the continental United States and Canada (Haack 2001). Native bark beetles pose serious threats to forests and can exacerbate additional disturbance events (Covington and Moore 1994). Southern pine beetle *(Dendroctonus frontalis)* (SPB) is an indigenous insect that has likely played a key role in shaping and maintaining pine forests of the Southern United States, and presents significant management challenges (SFIWC 2004).

SPB aggressively attacks healthy or stressed trees by attacking *en masse* and overwhelming host defenses. Tree mortality is required for successful beetle reproduction (Payne 1980). Loblolly pine *(Pinus taeda)* and shortleaf pine *(P. echinata)* are among the most commercially important timber species in the southern region (Barker and Langdon 1990), and are favored hosts (Payne 1980). Pine stands that are dense and those under increased abiotic stresses are most susceptible to losses by SPB infestation (Belanger 1980). During beetle population outbreaks, extensive overstory mortality of pines can occur.

Pine mortality can be reduced by suppression of SPB through cutting infested and susceptible pines nearby. A common suppression approach is cut-and-leave, which calls for felling all infested pines, plus a buffer strip of uninfested pines (≥ 10 cm in diameter), and leaving the felled pines in place at the front of the expanding infestation (Billings 1980). In effect, the cut-and-leave approach creates a buffer strip that disperses concentrated beetle populations and limits centralized attacks on susceptible pines.

Following SPB overstory mortality and cut-and-leave suppression, excessive coarse woody debris accumulates on the forest floor, a condition that leads to increased fuel loads and potentially devastating fire activity (Pyne and others 1996). In the Southeastern United States, wildfire is a common disturbance that can eliminate late-successional plant species and shift stand composition to more early-successional species (Oliver and Larson 1990). Fire disturbance disrupts the forest floor, creates favorable seedbed conditions (Shelton and Cain 2000), promotes growth and survival of shade-intolerant species such as loblolly and shortleaf pine, and influences plant diversity (Allen and Wyleto 1983).

SPB activity increases the incidence of wildfire. In combination, the two disturbance agents (SPB and wildfire) are postulated to have influenced the composition and structure of historic southern pine forests (Schowalter and others 1981). The revegetation of SPB-killed stands, and the influence of SPB mortality and/or control on subsequent forest composition and structure, has received little attention (see Balch 1928, Clarke and others 2000, Harrington and others 2000).

Recent introductions of numerous exotic bark beetle species and a long history of widespread mortality from bark beetles in the United States (Furniss and Carolin 1977, Price and others 1992) have led us to question how bark beetle caused mortality, associated suppression, and natural disturbance regimes influence forest communities. Our objective was to assess how disturbances associated with bark beetle impact long-term vegetation succession in the forests of Southeastern United States. More specifically, we set out to assess the vegetation composition, measure forest stand structure, and predict forest stand succession in Kisatchie Hills Wilderness following SPB-caused overstory mortality, associated cut-and-leave suppression, and wildfire in a pine (*Pinus* spp.) with mixed hardwood stand and in a longleaf pine *(P. palustris)* stand.

We hypothesized that forest canopies dominated by pine and mixed hardwood will have limited regeneration of pine and other early-successional species because of remnant hardwoods restricting gap size. We predicted early-successional communities would be more prominent in plots dominated by pine because of continuous overstory mortality and reduced competition in the overstory and understory. Plots in pine-dominated canopies were expected to maintain pine composition, in contrast to plots with a mixed forest type which we expected to shift to hardwoods.

Methods

Site Description

In 1984-85, > 1700 ha of pine forests on the Western Gulf Coastal Plain in the Kisatchie Hills Wilderness (Natchitoches Parish, LA) suffered extensive overstory mortality due to SPB (fig. 1). The 3250 ha Kisatchie Hills Wilderness (Kisatchie National Forest, central LA) is characterized by gently sloping terrain with forest canopies dominated by loblolly pine, longleaf pine, mixed pine-hardwood, and upland hardwood. Climatologically, it is characterized by mean annual maximum temperature of 24.7 °C with a minimum mean temperature of 12.6 °C, and annual precipitation of 140 cm (National Weather Service 2001).

In Kisatchie Hills, SPB infestations initially covered ~147 ha before suppression tactics were implemented. To suppress the rapidly expanding infestations, 70 cut-and-leave suppression events occurred during the 2-year period and encompassed the majority of the 1700 ha beetle disturbance (Nettleton and others 1988). In 1987, a high-intensity wildfire covering 3,000 ha caused overstory mortality and engulfed most of the beetle disturbed area within Kisatchie Hills, including the longleaf pine stand (Clarke 1995) (fig. 1). The wildfire began in previously disturbed SPB stands and expanded into undisturbed forest (489 ha), and was eventually contained by hiking trails and the wilderness boundary. A second low-intensity wildfire occurred in March 2000, covering 633 ha, including the pine-mixed hardwood stand. Because these wildfires occurred within wilderness boundaries, limited information on fire characteristics is available; fire intensity and speed of spread are unknown. As a result, fire intensity classifications are not direct measures and represent general groupings that were defined by pine fuel load, time of year, and occurrence of fire following pine mortality. In fall 1985, a study was established to assess plant succession following the bark beetle outbreak and associated suppression (fig. 2) (Pearson and Martin 1991); this study was subsequently disturbed by a low-intensity wildfire in 2000. Plots established in 1985 were located in a pine-mixed hardwood stand with SPB-caused overstory mortality and cut-and-leave suppression, and were part of the 2000 wildfire. Overstory trees in the pine-mixed hardwood stand were 50 years old at the time of the SPB outbreak and suppression events and classified as yellow pine (loblolly, shortleaf, and longleaf pines) and mixed hardwood canopies.

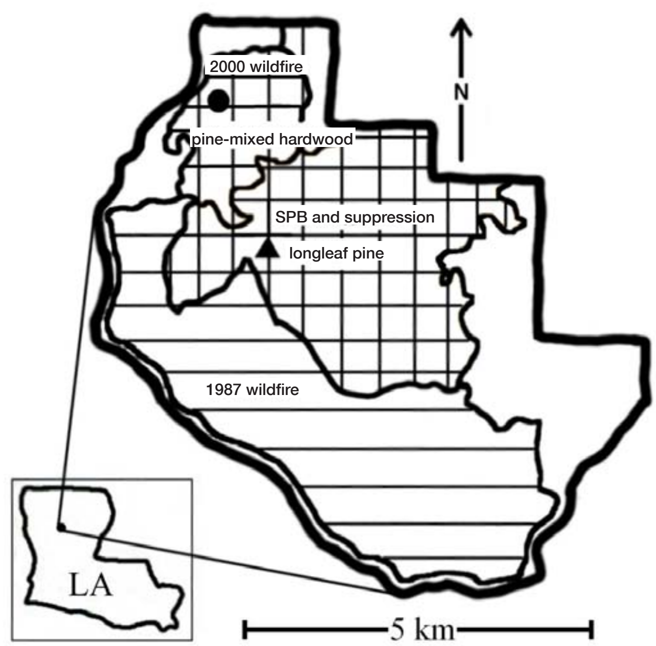
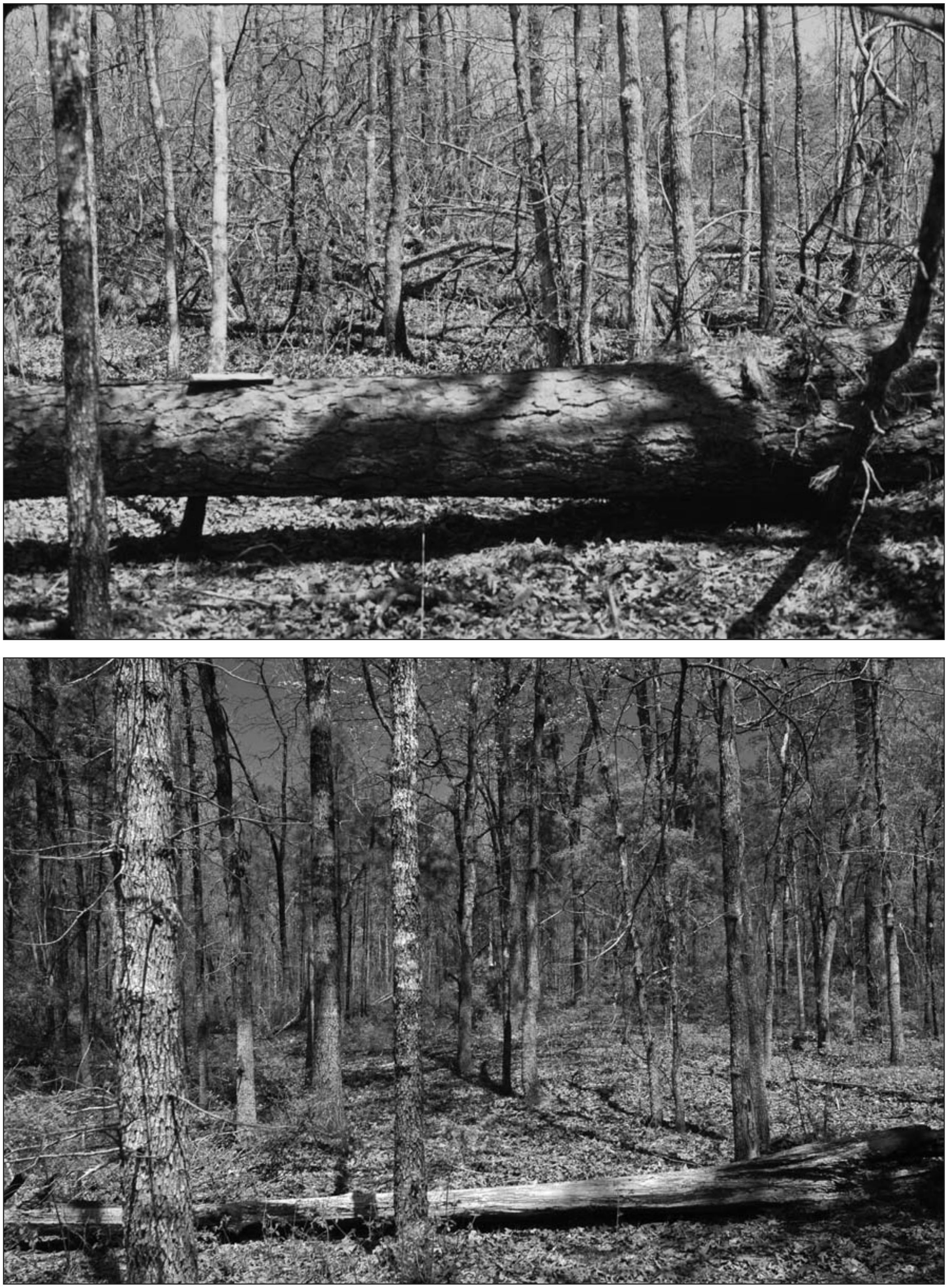


Figure 1—Kisatchie Hills Wilderness Area (Kisatchie National Forest, LA), showing the longleaf pine stand (▲) and pine-mixed hardwood stand (•) each with southern pine beetle-caused mortality (SPB), associated suppression, and wildfire. Vertical lines represent the extent of the 1984-85 SPB suppression, whereas horizontal lines depict the 1987 and 2000 wildfires.



(A)

(B)

Figure 2—Forest stand composition following SPB-caused mortality and associated suppression in pine forests in Kisatchie Hills Wilderness Area imaged (A) 2 years post-disturbance (1989) (photo by Alton Martin Jr.), and (B) from the same perspective 16 years post-disturbance (2003) (photo by Eric Vallery). Note vegetation succession and the prevalence of hardwoods.

A second study was established after the 1987 wildfire disturbance to the beetle-impacted areas, and examined interactions between SPB and fire in shaping forest succession (fig. 3) (Pearson and Martin 1991). The second study area, established in 1987, was dominated by longleaf pine and consisted of SPB-caused overstory mortality, cut-and-leave suppression, and the 1989 wildfire (figs. 1, 2, and 3). Canopy trees in the longleaf pine stand were 60 years old (USDA Forest Service 1985). No other major disturbances have occurred in these stands following the SPB outbreak and wildfires. In both 1985 and 1987, three plots were assigned in each disturbed stand, with each plot consisting of three parallel 30.5 m transects, separated by > 7.6 m. Each set of three parallel transects were considered a plot and were grouped as an experimental unit within each stand. Plots were separated by > 15.2 m within the stand, and were at least 50 m from the stand edge. Plots established in the mid-1980s span an area within each stand ≤ 1 ha. In each forest type, replicates were established within an individual stand boundary.

The dissimilar forest types, variable fire intensities, and different time of fire occurrence did not allow us to compare the two forest stands established from the initial study. The initial project design further complicated statistical analyses by violating the assumption of independence and by lacking replication (Hulbert 1984). In spite of the limitations to the initial study, the ability to assess the same plots using the same methodologies 16 and 14 years later creates a unique opportunity to monitor vegetation succession. As a result, we focused on the change in forest composition and structure (figs. 2 and 3) following each disturbance regime for the two different stand classifications.

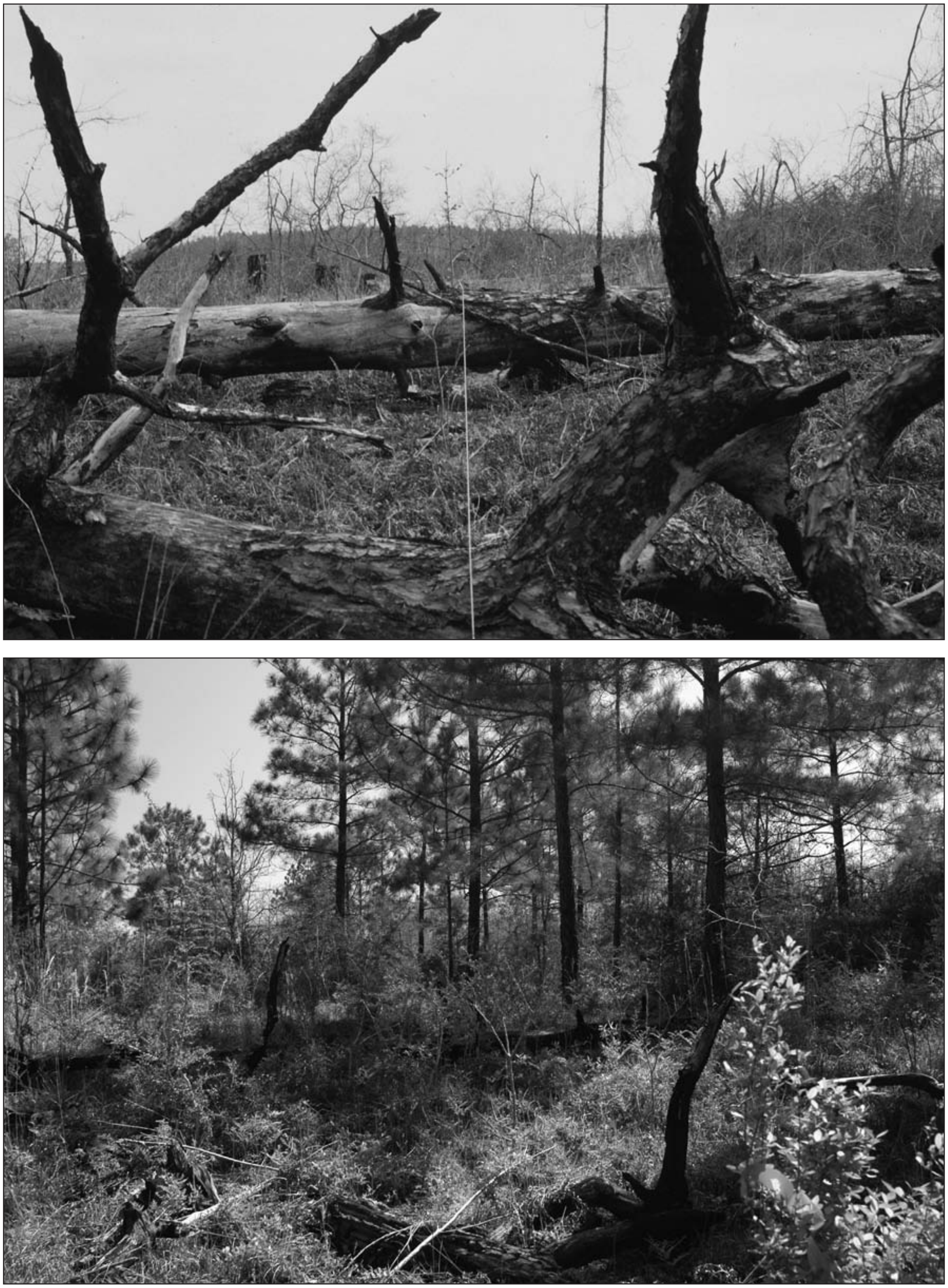
Vegetation and Stand Structure

Annual vegetation assessments began in 1985 in the pine-mixed hardwood stand and in 1987 in the longleaf pine stand. The assessments continued through 1989. Plant composition and stand structure from pre-disturbed or undisturbed pine stands (controls) were not assessed. In 2003, 18 years following the initial census, plots were re-censused using original methodology (Parker and Harris 1959). Each permanently located transect in each stand had 100 points designated for vegetation assessment at 0.3 m intervals. There were 300 points within each plot for vegetation assessment, for a total of 900 points per stand treatment. At each point the percent of bare soil, rock, leaf litter, coarse woody debris (> 6 cm diameter), and vegetative cover were assessed by viewing through a 0.02 m diameter circular loop positioned 0.3 m above the ground (Parker and Harris 1959). Plants with foliage within the sample loop were identified by species and used to compute plant composition. Plant cover was recorded if vegetation fell within the loop, regardless of aboveground height, using the following classification scheme: grasses (Families: Poaceae and Cyperaceae), forbs (non-grass herbaceous species), shrubs (woody species < 10 m and woody vines), and trees (woody species > 10 m). Woody plant cover was included if it was ≤ 0.3 m in height. To record woody plants > 0.3 m, a line-intercept method was used at the same 0.3 m intervals along the same transects (Canfield 1941). Using this approach, an imaginary line was extended vertically. All species intercepting this line were used to calculate plant composition using absolute frequency. At 7.6, 15.2, and 22.9 m divisions along each transect, canopy cover was recorded in each cardinal direction using a spherical densiometer (Lemmon 1956). In the censuses of the 1980s, basal area (m^2/ ha) of pines and hardwood species were calculated using a 5.7 m^2/ ha basal area factor (10-factor prism) at the midpoint of each transect. Only trees > 12.7 cm d.b.h. were used to assess pine and hardwood species basal area.

In the 2003 census only, three 0.04 ha fixed-size plots were established in the middle of one randomly chosen transect at each plot to further describe stand characteristics and the canopy composition (USDA Forest Service 2003) in each disturbance regime. All woody species (≥ 12.7 cm d.b.h.) were measured for diameter (d.b.h.), height (m), and frequency in the 0.04 ha plot following protocols of the Common Stand Exam (USDA Forest Service 2003). Canopy species composition and basal area (m^2/ha) were then assessed in each 0.04 ha plot. In addition, within each 0.04 ha plot, five 0.0004 ha subplots were positioned centrally, and in the four corners of the whole plot to survey the understory woody species (< 12.7 cm d.b.h.), where height, diameter (d.b.h., if applicable), and count were assessed for each species (USDA Forest Service 2003). Data from the 0.04 and 0.0004 ha plots were used only to calculate forest stand structure.

Forest Modeling

Whole and subplot vegetation measurements from the 2003 assessments were modeled 50 years into the future using the southern variant of the Forest Vegetation Simulator (FVS) and assuming no further disturbance (USDA Forest Service 2001). We modeled the forest type, basal area for hardwoods, and the pine component for each forest stand. Assessed tree data and landscape variables, including species, d.b.h., height, height to crown, radial growth, and ecological region, were incorporated into FVS to calibrate and model forest



(A)

(B)

Figure 3—Forest stand composition following SPB-caused mortality, associated suppression, and wildfire in pine forests in Kisatchie Hills Wilderness Area imaged (A) 2 years post-disturbance (1991) (photo by Alton Martin Jr.), and (B) from the same perspective 14 years post-disturbance (2003) (photo by Eric Vallery). Note vegetation succession and the prevalence and patchiness of pines in the 2003 photo.

stand succession on a 5-year cycle (Donnelly and others 2001). Predicted forest type and stand characteristics were obtained from the FVS by using the main output and the stand and stocking simulators.

The FVS is an individual-tree nonspatial forest growth model built from the core model Prognosis (Stage 1973), and adapted from previous models developed for forests of the Western United States. Although the southern variant of the FVS is a relatively new extension, FVS was found to be most adaptable to key features identified among several other individual-tree growth models (Robinson and Monserud 2003). FVS incorporates site-specific variables for calibration. Furthermore, FVS is adequate for simulating long-term processes where growth is the main component (Teck and others 1996).

Analyses

We compared vegetation from 2 years post-disturbance, 1987 for the pine-mixed hardwood stand and 1989 for the longleaf pine stand, to assessments from 2003. Plant species abundance was assessed, and richness, diversity, and evenness calculated for all transects for each year under analysis. Individual abundance (total number of tallies) and richness for grasses, forbs, shrubs, and trees were calculated, along with total plant abundance and richness. Diversity and evenness were calculated for total plant communities. Diversity was calculated using the Shannon index ($H' = -\Sigma p_i \ln p_i$) where p_i is the relative abundance of the *i*th species per transect (Magurran 1988). Evenness was calculated as J' ($J' = H'/lnS$) where S, richness, is the number of species sampled along a transect (Magurran 1988). The calculated parameters are a measure of relative ground cover at the 0.3 m increments along the transects,

Table 1—Vegetation composition following southern pine beetle-caused overstory mortality, cut-and-leave suppression, and wildfire in a pine-mixed hardwood stand and a longleaf pine stand

	Pine-mixed hardwood			Longleaf pine		
Parameter	Effect	1987	2003	Effect	1989	2003
A. Plant community						
Abundance	$30.9_{1, 2}$/ ***	31 (6.23)	184 (12.6)	$123_{1, 2}$/ ***	123 (11.9)	227 (8.5)
Richness	$17.6_{1, 2}$/ **	9 (1.07)	20 (1.4)	$79.9_{1, 2}$/ ***	16 (0.93)	28 (1.36)
Diversity	$6.54_{1, 2}$/ n.s.	1.79 (0.14)	2.24 (0.11)	$2.46_{1, 2}$/ n.s.	2.11 (0.14)	2.46 (0.1)
Evenness	$17.9_{1, 2}$/ **	0.87 (0.02)	0.75 (0.03)	$0.2_{1, 2}$/ n.s.	0.76 (0.04)	0.73 (0.02)
B. Grasses						
Abundance	$0.23_{1, 2}$/ n.s.	5 (2.1)	5 (1.05)	$0.05_{1, 2}$/ n.s.	43 (7.2)	39 (8.66)
Richness	$3.18_{1, 2}$/ n.s.	1 (0.35)	3 (0.62)	$2.38_{1, 2}$/ n.s.	5 (0.73)	7 (0.96)
C. Forbs						
Abundance	$2.68_{1, 2}$/ n.s.	2 (1.43)	6 (3.45)	$6.39_{1, 2}$/ n.s.	30 (4.71)	37 (5.14)
Richness	$2.29_{1, 2}$/ n.s.	0 (0.24)	1 (0.29)	$36.9_{1, 2}$/ **	4 (0.36)	10 (0.74)
D. Shrubs						
Abundance	$70.9_{1, 2}$/ ***	13 (3.39)	61 (7.31)	$128_{1, 2}$/ ***	32 (6.38)	80 (10.9)
Richness	$23.9_{1, 2}$/ **	4 (0.74)	9 (0.65)	$60.8_{1, 2}$/ **	5 (0.29)	8 (0.50)
E. Trees						
Abundance	$129_{1, 2}$/ ***	8 (1.24)	118 (6.94)	$42.1_{1, 2}$/ **	17 (3.99)	72 (9.62)
Richness	$123_{1, 2}$/ ***	3 (0.39)	7 (0.75)	$5.26_{1, 2}$/ n.s.	2 (0.32)	4 (0.77)
F. Ground cover (percent)						
Bare soil	$1.00_{1, 2}$/ n.s.	0 (0)	0.3 (0.11)	$0_{1, 2}$/ n.s.	4.7 (0.6)	4.9 (0.62)
Rock	$1.00_{1, 2}$/ n.s.	0.5 (0.23)	0.9 (0.3)	—	0 (0)	0 (0)
Leaf-litter	$4.65_{1, 2}$/ n.s.	82.8 (1.07)	80.6 (1.01)	$31.8_{1, 2}$/ **	46.1 (1.18)	68.8 (0.97)
Coarse woody debris	$7.62_{1, 2}$/ n.s.	7.6 (0.88)	1.4 (0.39)	$7.30_{1, 2}$/ n.s.	11.8 (1.07)	0.4 (0.22)
Vegetation	$6.32_{1, 2}$/ n.s.	8.7 (0.69)	16.7 (0.91)	$4.01_{1, 2}$/ n.s.	37.3 (1.14)	25.7 (0.89)

Means (s.e.) from analysis: F_{df} / P-value.

n.s.= $P \geq 0.1$.

*** = $P \leq 0.01$.

** = $P \leq 0.05$.

— = not available for statistical analysis.

and may not be exact counts of species density (Pearson and Martin 1991). In our case, species abundance is actually the frequency of tallies along a transect. Only data collected from transects were utilized to calculate plant indices.

A mixed model analysis of variance (PROC MIXED, SAS 1997) was used to describe differences in plant abundance, diversity, richness, evenness, canopy cover, and ground cover within each disturbance regime over the 16-year (pine-mixed hardwood) and 14-year (longleaf pine) durations of the study. The change in time was used as the fixed effect, with transects designated as random effects. Three transects were treated as a plot and grouped as an experimental unit for each disturbance regime (N=3). Data was log transformed if underlying assumptions were not met for the analyses of variance. Treatment effects were considered statistically significant if $P \leq 0.05$. Forest characteristics (pine basal area, hardwood basal area, and canopy cover) were also analyzed using a mixed model analysis of variance (PROC MIXED, SAS 1997). The 1980s data was compared to 2003, and the 2003 data to predicted 2053 FVS data. Pine and hardwood basal area were calculated only from the 0.04 ha plots for the 2003 analyses. Whole plots, rather than transects, were used as random effects.

Results

A total of 5,047 plants representing 117 species were tallied from the transects over the 16-year study, including 29 grasses, 33 forbs, 30 shrubs, and 25 tree species (app. 1). Grasses comprised 16 percent of the total plants surveyed (820 tallies; app. 1A). Forbs comprised 13 percent of the total plants surveyed, with 666 tallies (app. 1B). Shrubs comprised 33 percent of the total plants, with 1,681 tallies counted (app. 1C). Trees were the most abundant vegetative class surveyed, comprising 39 percent of individuals (1,946 tallies; app. 1D).

Pine-Mixed Hardwood

Plant abundance and richness significantly increased by 494 percent and 92 percent in the pine-mixed hardwood, respectively, from 1987 to 2003 (table 1A). Mortality to the pine overstory and wildfire also decreased plant evenness 14 percent, whereas plant diversity did not differ (table 1A).

Forty-nine individual grasses representing four grass species were observed in 1987 and 42 grasses from 12 species in 2003 (app. 1A). The two most abundant grass species in the pine-mixed hardwood stand in 1987 were little bluestem *(Schizachyrium scoparium)* and longleaf woodoats *(Chasmanthium sessiliflorum),* whereas no grass species dominated in 2003.

Twenty-one forbs representing two species were observed in 1989 and 59 forbs representing eight species in 2003 (app. 1B). Western bracken fern *(Pteridium aquilinum)* was overwhelmingly the most abundant forb species and increased in occurrence from 1987 to 2003. Grass and forb species abundance and richness did not significantly vary over the duration of the study (tables 1B and 1C).

In pine-mixed hardwood plots, 125 shrubs comprising 10 species were surveyed in 1987 and 543 shrubs from 23 species in 2003 (app. 1C). The two most abundant shrub species in 1987 were Elliott's blueberry *(Vaccinium elliottii)* and muscadine *(Vitis rotundifolia).* In 2003, yaupon *(Ilex vomitoria)* and farkleberry *(Vaccinium arboretum)* were the most abundant shrub species. Over the 16-year period, shrub abundance and richness increased by 79 percent and 56 percent in the pine-mixed hardwood stand, respectively (table 1D).

Eighty-four trees representing nine species were tallied in 1987 and 1,058 trees from 18 species in 2003 (app. 1D). The two most abundant tree species in 1987 were loblolly pine, followed by southern red oak *(Quercus falcata).* In 2003, post oak *(Q. stellata)* and mockernut hickory *(Carya tomentosa)* were the most abundant tree species. Bitternut hickory *(C. cordiformis)* and sweetgum *(Liquidambar styraciflua)* were also abundant species (> 50 frequency) in 2003. Tree abundance increased by 1375 percent from 1987 to 2003 (table 1E). Tree species richness significantly increased by 120 percent over the same time period (table 1E).

Ground cover did not differ over the study period in the pine-mixed hardwood stand. However, coarse woody debris decreased by 57 percent and vegetation cover increased by 92 percent from 1987 to 2003, but the changes were not significant. Pine regeneration was evident by 2003 where hardwood basal area declined, but neither was statistically significant. Canopy cover significantly increased by 146 percent from the initial assessments to 2003 (table 2A).

The FVS designated the pine-mixed hardwood stand as a loblolly pine-hardwood forest type in the 2003 stand census, and the forest type did not change throughout the modeling projection. Dominant species were predicted to be southern red oak, loblolly pine, and mockernut hickory, in that order. Basal area increased by 247 percent for pine and 65 percent for hardwoods during the model projection, but the increases were not significant.

Longleaf Pine

Plant abundance significantly increased by 84 percent over the 16-year duration (table 1A). Similar increases were observed for plant richness over the same time period (92 percent) (table 1A). The interaction of overstory pine mortality and fire did not impact plant diversity or plant evenness from 1989 to 2003. In the longleaf pine stand, 384 grasses from 14 species were tallied in 1989 and 345 grasses from 20 species in 2003 (app. 1A). Panicgrass (*Panicum* spp.) and little bluestem were the most abundant grasses in 1989, but little bluestem was the most abundant in 2003. Grass abundance and richness did not vary from 1989 to 2003 (table 1B).

In longleaf pine plots, 263 forbs comprising 12 species were assessed in 1989 and 323 forbs from 28 species in 2003 (app. 1B). Bracken fern was the most abundant forb, but slightly decreased in abundance from 1989 to 2003. Wildfire and canopy loss increased forb species richness (150 percent) from 1989 to 2003 (table 1C).

Two hundred ninety-four shrubs representing 13 species were surveyed in 1989 and 719 shrubs from 17 species in 2003 (app. 1C). In 1989, yaupon and winged sumac *(Rhus copallinum* L. var. *latifolia)* were the two most abundant species. Yaupon was again the most abundant species in 2003 with farkleberry second in abundance. Shrub abundance significantly increased by 150 percent from 1989 to 2003, and shrub species richness increased by 89 percent (table 1D).

In longleaf pine plots, 164 trees comprising six tree species were observed in 1989, and 640 trees comprising 17 species in 2003 (app. 1D). Bluejack oak *(Q. incana)* and post oak were the two most abundant species in 1989 and 2003. In 2003, loblolly pine and longleaf pine were also prevalent. The interacting disturbances significantly increased tree abundance by 935 percent from 1989 to 2003 (table 1E). The accumulation of leaf-litter in the longleaf pine stand was significant (49 percent) (table 1F). Woody debris decreased by 97 percent from 1989 to 2003, but the decline was not significant. Pine and hardwood basal area increased from 1989 to 2003, but neither were significant. Canopy cover significantly increased by 1,700 percent from the initial assessments to 2003 (table 2A).

In the longleaf pine stand, FVS designated the forest type as post oak-bluejack oak in 2003. The post oak-bluejack oak forest type shifted to a loblolly-hardwood forest type before transitioning to and maintaining a loblolly pine canopy in the 2053 projection. The predicted canopy is dominated by loblolly pine and bluejack oak; longleaf pine is also evident in the canopy while post oak is evident in the midstory.

Discussion

This was an opportunistic study whereby we utilized the framework from a preexisting study established in the mid-1980s to assess the successional trajectory following mortality caused by SPB suppression measures and wildfire. In spite of limitations associated with the original experimental design, we were able to use the exact methodologies at the exact locations to assess vegetation succession. Although the constraints imposed by the original study limit the inferences we are able to make (Hulbert

Table 2—Stand characteristics (A) and predicted stand characteristics (B) following southern pine beetle-caused mortality, cut-and-leave suppression, and wildfire in a pine-mixed hardwood stand and in a longleaf pine stand

	Pine-mixed hardwood			Longleaf pine		
A. Stand characteristics	Year effect	1987	2003	Year effect	1989	2003
Pine basal area (m^2/ha)	$2.41_{1,16}$/ n.s.	0.0(0)	6.3(4.07)	$5.37_{1,16}$/ n.s.	0.0 (0)	0.9 (0.39)
Hardwood basal area (m^2/ha)	$1.27_{1,16}$/ n.s.	11.7(3.39)	8.4(4.05)	$3.47_{1,16}$/ n.s.	0.51 (0.51)	0.2 (0.10)
Canopy cover (percent)	$12.7_{1,16}$/ *	36.7(5.72)	90.3(2.11)	$14.9_{1,16}$/ *	3.6(1.46)	65 (6.5)
	Loblolly-hardwood				Post-blackjack oak	Loblolly pine
B. Predicted stand characteristics	Year effect	2003	2053	Year effect	2003	2053
Pine basal area (m^2/ha)	$8.46_{1,16}$/ n.s.	6.3 (4.07)	21.9 (7.89)	$1.87_{1,16}$/ n.s.	0.9 (0.39)	24.3 (13.4)
Hardwood basal area (m^2/ha)	$4.69_{1,16}$/ n.s.	8.4 (4.05)	13.9 (5.83)	$0.06_{1,16}$/ n.s.	0.2 (0.10)	15.5 (9.82)

Means (s.e.) from analysis: F_{df} / P-value.

n.s.= $P \geq 0.1$.

* = $P<0.1$.

1984), the opportunity to study forest succession using the original protocols under these interacting disturbance regimes was a strong impetus. Forest disturbance from SPB, suppression, and subsequent wildfire altered plant composition and stand characteristics after 14 years.

Pine-Mixed Hardwood

In the pine-mixed hardwood stand, loss of the codominant pine component increased the growing space and altered conditions on the forest floor. However, remnant hardwoods restricted gap size and limited growth of early successsion, shade-intolerant species, like grasses and forbs. Increases in total plant abundance and richness resulted from increases in the woody plant community, including yaupon, farkleberry, post oak, hickories, and sweetgum. The plant community became less evenly distributed, probably due to the dominance of the woody community. Elliott and others (1997) report a similar increase in plant richness but no change in plant diversity following a clearcut in southern Appalachia.

The early season (March) fire, coupled with the diminished fuel load from canopy mortality 14 years earlier, most likely impacted primarily understory vegetation, with only a limited influence on canopy vegetation. This allowed persistence of undisturbed hardwoods that decrease light exposure and air currents and prevent loss of soil moisture, promoting shade-tolerant and mesic-favoring woody plants, including Elliott's blueberry and muscadine, which were abundant in the pine-mixed hardwood plots (Gleason and Cronquist 1991, USDA NRCS 2005).

Post oak, two species of hickories, and sweetgum were prominent in the pine-mixed hardwood stand in 2003, but pine basal area was comparable to hardwood basal area. Modeling predicts the pine basal area to double, thus maintaining the pine-mixed hardwood stand, but with loblolly pine dominating instead of several pine species. Ten years after small-scale canopy disturbances caused by SPB, Balch (1928) reported pine dominated canopies were transitioning to similar pine-oak canopies in North Carolina. The pine-mixed hardwood stand in 2003 had a two-story structure with hardwoods in dominant positions in the canopy and pine and hardwood regeneration in the midstory. Similarly, mortality of small patches of pine caused by SPB also increased structural complexity in late-successional pine-hardwood stands (Harrington and others 2000). The interacting disturbances altered the initial even-aged stand, and reduced the susceptibility to stand replacing disturbances from future SPB outbreaks, thereby potentially enhancing forest health.

Longleaf Pine

Two years following widespread pine mortality, subsequent wildfire eliminated the pine and hardwood component, creating extensive gaps that favored pioneer and early-successional species in the longleaf pine stand. Significant increases in canopy cover from 1989 to 2003, and minimal hardwood basal area in 1989 (table 2A), accurately depict these widespread losses. Disturbances reduced competition and increased sunlight penetration which increased total plant abundance and richness, forb richness, and tree abundance. Similar increases in plant richness were documented following fire in a second growth pineland in northern Florida (Mehlman 1992). Wildfire can eliminate competition, create greater sun exposure, increase bare soil, and reduce soil moisture (Walker 1962). As we expected, fire promoted plant species that can colonize quickly and withstand dry conditions created by minimal canopy cover, as well as species otherwise associated with disturbed habitats (Gleason and Cronquist 1991, USDA NRCS 2005). The three dominant grasses in the longleaf pine stand, similar to old fields or dry areas, were panicgrass, little bluestem, and tapered rosette grass *(Dichanthelium acuminatum)*. The overwhelming abundance of bluestem, in particular *Andropogon* spp. and *Schizachyrium* spp., found in our longleaf pine plots are common to the fire-driven longleaf pine ecosystems of the Southeastern United States. These grass genera facilitate ignition and spread of fire during the growing season, sustaining longleaf pine composition (Landers 1991).

Bluejack and post oaks were the most abundant trees in 2003, with loblolly and longleaf pines in lower densities. Modeling predicts that the less abundant loblolly pine will eventually attain dominance, shifting the longleaf pine stand to loblolly pine. Loss of longleaf pine represents a loss of a highly desirable forest type, and also represents a shift from a less susceptible to a highly susceptible host of SPB.

The FVS predicts pine either as a dominant or codominant component in each forest type. Modeling predicts that the future forest (2053) having pine basal area of 21.9 m^2/ha in the loblolly pine-hardwood stand and 24.3 m^2/ha in the loblolly pine. Although model predictions forecast a forest moderately susceptible to SPB (Mason and others 1985), these dense pockets (of basal area) represent high hazards for SPB-caused mortality. The presence of scattered hardwoods may inhibit local spread of SPB within a stand (Hedden and Billings 1979), but hardwoods ultimately increase stress to pines by enhancing competition for resources, thereby escalating susceptibility to SPB.

Interacting disturbances from SPB, associated suppression, and wildfire sustained the pine component. But without additional management, stands are predicted to become increasingly susceptible to SPB-caused mortality. Modeling predicts loblolly pine to dominate in the initially disturbed longleaf pine stand, enhancing susceptibility to SPB, and understory grasses increase fuel loads, enhancing susceptibility to wildfire. SPB and wildfire have historically played critical roles in influencing the successional trajectories of southern forests, and our modeling suggests that these disturbances are likely to continue shaping southern forest composition and succession.

Acknowledgments

We thank Kisatchie Ranger District (Natchitoches, LA), U.S. Department of Agriculture Forest Service, Southern Research Station, Pineville, LA and James H. Scarborough for use of facilities during this project and Jason Pieratt (University of Kentucky) for consultation about statistical analysis. We thank Brian Strom and additional anonymous reviewers for reviewing an earlier draft of this manuscript. This research was supported by funds from the Forest Service Forest Health Protection and their Pest Trend Impact Plot System program, the Southern Research Station Forest Insect Research Work Unit, and McIntire Stennis funds from the Kentucky Agricultural Experiment Station. Research support was provided through PTIPS, Region 8 (2004-2006) and is published as Experiment Station Project 06-08-011.

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Appendix—Temporal changes in vegetation species in a pine (*Pinus* spp.)-mixed hardwood stand and a longleaf pine *(Pinus palustris)* stand suffering overstory mortality from southern pine beetle *(Dendroctonus frontalis)*-caused mortality, associated suppression, and subsequent wildfire

Species name	Common name	Pine-mixed hardwood		Longleaf pine	
		1987	2003	1989	2003
A. Grasses					
Family Cyperaceae					
Cyperus retrofractus	Rough flatsedge	0	0	8	0
Eleocharis spp.	Spikerush	0	0	2	0
Rhynchospora glomerata	Cluster beaksedge	0	0	1	1
Scleria ciliata	Fringed nutrush	0	5	8	7
Scleria oligantha	Littlehead nutrush	0	0	0	2
Family Poaceace					
Andropogon elliottii	Elliott's bluestem	2	0	3	0
Andropogon ternarius	Splitbeard bluestem	1	0	28	4
Andropogon virginicus	Broomsedge bluestem	0	0	0	13
Aristida purpurascens	Arrowfeather threeawn	0	1	7	12
Aristida spp.	Threeawns	0	0	1	1
Chasmanthium laxum	Slender woodoats	0	1	0	0
Chasmanthium sessiliflorum	Longleaf woodoats	20	9	0	0
Dichanthelium aciculare	Needleleaf rosette grass	0	2	0	7
Dichanthelium acuminatum	Tapered rosette grass	0	1	0	23
Dichanthelium boscii	Bosc's panicgrass	0	0	0	1
Dichanthelium scoparium	Velvet panicum	0	5	0	2
Dichanthelium sphaerocarpon	Roundseed panicgrass	0	0	0	3
Dichanthelium spp.	Rosette grass	0	1	0	1
Digitaria ischaemum	Smooth crabgrass	0	0	4	0
Eragrostis spectabilis	Purple lovegrass	0	0	0	2
Gymnopogon ambiguus	Bearded skeletongrass	0	1	0	3
Muhlenbergia expansa	Cutover muhly	0	0	6	1
Panicum spp.	Panicgrass	0	0	221	0
Paspalum floridanum	Florida paspalum	0	0	0	1
Paspalum plicatulum	Brownseed paspalum	0	0	1	0
Polypogon spp.	Beard grass	0	6	0	0
Schizachyrium scoparium	Little bluestem	26	7	87	247
Schizachyrium tenerum	Slender little bluestem	0	0	0	12
Sorghastrum nutans	Indiangrass	0	3	7	2
Total grass and graminoid plants		49	42	384	345
B. Forbs					
Family Aristolochiaceae					
Aristolochia serpentaria	Virginia snakeroot	0	1	0	4
Family Asteraceae					
Aster dumosus	Rice button aster	0	0	0	1
Erigeron canadensis	Canadian horseweed	0	0	11	0
Helianthus angustifolius	Swamp sunflower	0	0	5	3
Heterotheca graminifolia	Narrowleaf silkgrass	1	0	1	20
Heterotheca pilosa	Soft goldenaster	0	0	1	3
Kuhnia eupatorioides	False boneset	0	0	0	1
Liatris pycnostachya	Prairie blazing star	0	0	0	2
Rudbeckia hirta	Blackeyed Susan	0	0	0	1
Solidago odora	Anisescented goldenrod	0	1	17	12
Family Cistaceae					
Lechea minor	Thymeleaf pinweed	0	0	1	0
Family Dennstaedtiaceae					
Pteridium aquilinum	Western bracken fern	20	46	208	178
Family Euphorbiaceae					
Acalypha gracilens	Slender threeseed mercury	0	0	0	1
Euphorbia corollata	Flowering spurge	0	0	0	8
Tragia smallii	Small's noseburn	0	1	0	31
Tragia urens	Wavyleaf noseburn	0	0	0	5
Tragia urticifolia	Nettleleaf noseburn	0	1	1	9
Family Fabaceae					
Cassia fasciculata	Sleepingplant	0	0	14	0
Clitoria mariana	Atlantic pigeon-wings	0	0	0	4
Desmodium lineatum	Sand ticktrefoil	0	0	0	1
Galactia erecta	Erect milkpea	0	0	0	4

continued

Appendix—Temporal changes in vegetation species in a pine (*Pinus* spp.)-mixed hardwood stand and a longleaf pine *(Pinus palustris)* stand suffering overstory mortality from southern pine beetle *(Dendroctonus frontalis)*-caused mortality, associated suppression, and subsequent wildfire *(continued)*

Species name	Common name	Pine-mixed hardwood		Longleaf pine	
		1987	2003	1989	2003
Family Fabaceae (continued)					
Galactia volubilis	Downy milkpea	0	1	0	4
Lespedeza virginica	Slender lespedeza	0	1	0	1
Rhynchosia difformis	Doubleform snoutbean	0	0	0	2
Rhynchosia reniformis	Dollarleaf	0	0	0	2
Stylosanthes biflora	Sidebeak pencilflower	0	0	0	6
Tephrosia virginiana	Virginia tephorsia	0	0	2	11
Family Lamiaceae					
Pycnanthemum albescens	White mountainmint	0	0	1	4
Family Lobeliaceae					
Lobelia puberula	Downy lobelia	0	0	0	1
Family Rubiaceae					
Galium pilosum	Hairy bedstraw	0	0	0	1
Mitchella repens	Partridgeberry	0	7	0	0
Family Scophulariaceae					
Agalinis spp.	False foxglove	0	0	0	3
Family Selaginellaceae					
Seliginella spp.	Spikemoss	0	0	1	0
Total forbs		21	59	263	323
C. Shrubs					
Family Agavaceae					
Yucca louisianensis	Gulf Coast yucca	0	0	0	3
Family Anacardiaceace					
Rhus aromatica	Fragrant sumac	0	3	0	0
Rhus copallinum var. *latifolia*	Winged sumac	0	3	40	28
Toxicodendron radicans	Eastern poison ivy	0	2	0	0
Toxicodendron toxicarium	Atlantic poison oak	0	0	0	10
Family Aquifoliaceae					
Ilex vomitoria	Yaupon	14	144	148	417
Family Bignoniaceae					
Bignonia capreolata	Crossvine	1	7	0	0
Family Caprifoliaceae					
Viburnum dentatum	Southern arrowwood	0	3	0	0
Viburnum rufidulum	Rusty blackhaw	0	6	0	0
Family Ericaceae					
Rhododendron canescens	Sweet mountain azalea	10	17	0	0
Vaccinium arboreum	Farkleberry	5	116	32	89
Vaccinium elliottii	Elliott's blueberry	46	41	4	49
Vaccinium stamineum	Deerberry	0	15	36	63
Vaccinium virgatum	Small flower blueberry	7	63	0	4
Family Hypericaceae					
Hypericum hypericoides	St. Andrews cross	2	0	1	0
Family Smilacaceae					
Smilax bona-nox	Saw greenbrier	0	1	0	1
Smilax glauca	Cat greenbrier	2	13	12	13
Smilax pumila	Sarsparilla-vine	10	17	0	0
Smilax rotundifolia	Roundleaf greenbrier	0	4	0	0
Family Loganiaceae					
Gelsemium sempervirens	Evening trumpetflower	1	9	9	21
Family Rhamnaceae					
Berchemia scandens	Alabama supplejack	1	0	0	0
Ceanothus americanus	New Jersey tea	0	0	1	3
Family Rosaceae					
Crataegus marshallii	Parsley hawthorn	0	0	0	1
Crataegus spathulata	Littlehip hawthorn	0	1	0	0
Rubus spp.	Blackberry	0	0	0	1
Rubus trivialis	Southern dewberry	0	0	3	0
Family Styracaceae					
Styrax grandifolius	Bigleaf snowbell	8	20	0	0
Family Verbenaceae					
Callicarpa americana	American beautyberry	1	16	1	8

continued

Appendix—Temporal changes in vegetation species in a pine (*Pinus* spp.)-mixed hardwood stand and a longleaf pine *(Pinus palustris)* stand suffering overstory mortality from southern pine beetle *(Dendroctonus frontalis)*-caused mortality, associated suppression, and subsequent wildfire *(continued)*

Species name	Common name	Pine-mixed hardwood		Longleaf pine	
		1987	2003	1989	2003
Family Vitaceae					
Vitis aestivalis	Summer grape	2	8	3	1
Vitis rotundifolia	Muscadine	16	40	4	5
Total shrubs		125	543	294	719
D. Trees					
Family Aceraceae					
Acer rubrum	Red maple	0	22	0	1
Family Aquifoliaceae					
Ilex opaca	American holly	2	0	0	0
Family Cornaceae					
Cornus florida	Flowering dogwood	7	43	0	7
Family Ebenaceae					
Diospyros virginiana	Common persimmon	0	0	0	1
Family Fagaceae					
Quercus falcata	Southern red oak	9	191	13	51
Quercus incana	Bluejack oak	0	0	94	245
Quercus marilandica	Blackjack oak	0	8	0	0
Quercus nigra	Water oak	0	9	0	0
Quercus stellata	Post oak	4	151	24	88
Family Hamamelidaceae					
Liquidambar styraciflua	Sweetgum	1	54	0	1
Family Juglandaceae					
Carya cordiformis	Bitternut hickory	0	75	0	0
Carya tomentosa	Mockernut hickory	0	143	0	4
Family Lauraceae					
Persea borbonia	Redbay	0	0	0	3
Sassafras albidum	Sassafras	0	0	18	11
Family Myricaceae					
Myrica cerifera	Wax myrtle	6	11	7	11
Family Nyssaceae					
Nyssa sylvatica	Blackgum	2	6	0	3
Family Oleaceae					
Chionanthus virginicus	White fringetree	0	4	0	6
Fraxinus pennsylvanica	Green ash	0	4	0	0
Family Pinaceae					
Pinus echinata	Shortleaf pine	0	11	0	11
Pinus palustris	Longleaf pine	0	0	0	26
Pinus taeda	Loblolly pine	46	361	0	56
Family Rosaceae					
Prunus serotina	Black cherry	0	4	8	0
Prunus umbellata	Hog plum	0	0	0	1
Family Sapotaceae					
Bumelia lanuginosa	Gum bully	5	1	0	0
Family Styracaceae					
Halesia diptera	Two-wing silverbell	0	5	0	0
Total trees		84	1,058	164	640
Total individuals		278	1,753	1,105	1,911

Species names follow USDA, NCRS PLANTS database (2005).

Numbers indicate frequency of tallies along transects for A. Grasses (Families Poaceae and Cyperaceae), B. Forbs (non-grass herbaceous species), C. Shrubs (woody plants < 10m), and D. Trees (woody plants > 10m).

Coleman, T.W.; Martin, Alton, Jr.; Meeker, J.R. [and others]. 2010. Disturbance from southern pine beetle, suppression, and wildfire affects vegetation composition in central Louisiana: a case study. Gen. Tech. Rep. SRS–129. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 15 p.

We assessed plant composition and forest succession following tree mortality from infestation of southern pine beetle (*Dendroctonus frontalis*), associated suppression, and wildfire in two forest types, pine (*Pinus* spp.) with mixed hardwood and longleaf pine (*P. palustris*). In this case study, vegetation was assessed in 2003 using methodology and experimental framework established 16 years earlier. We examined changes in vegetation composition from the 1980s to 2003 in each forest stand type and used the Forest Vegetation Simulator to predict forest succession.

In the pine-hardwood stand, total plant and woody plant abundance and richness increased over the study while total plant evenness decreased. The Forest Vegetation Simulator predicts the pine-mixed hardwood will shift to loblolly pine-hardwood after 50 years. In the longleaf pine stand, total plant abundance and richness increased. The interacting disturbances enhanced forb, shrub, and tree abundance. Forb and shrub species richness also increased. Modeling predicts the longleaf pine stand will shift to loblolly pine (*P. taeda*) following the disturbance events. Although stand predictions are different for each initial forest type, predicted pine and hardwood basal area represent high susceptibility to future SPB outbreaks.

The interaction of these three disturbance events (beetle infestation, associated suppression, and wildfire) appears to maintain pine composition, but also the potential for additional SPB-caused mortality, though thinning may reduce the susceptibility of these stands to bark beetle disturbance. The unique opportunity to assess interacting disturbances and natural succession was the motivation for our study, but our inferences are limited due to constraints of the experimental design.

Keywords: Cut-and-leave suppression, Forest Vegetation Simulator, loblolly pine, southern pine beetle, wildfire.