RESEARCH NOTE

•

Structural Characteristics of Late-Successional Pine-Hardwood Forest Following Recent Infestation by Southern Pine Beetle in the Georgia Piedmont, USA

Timothy B. Harrington[1]
Mingguang Xu
Daniel B.Warnell School of Forest Resources
University of Georgia
D.W. Brooks Drive
Athens, Georgia 30602-2152 USA

M. Boyd Edwards
USDA Forest Service
Southern Research Station
320 Green Street
Athens, Georgia 30602 USA
oikos2@mindspring.com

•

[1] Corresponding author e-mail: tharring@arches.uga.edu

Natural Areas Journal 20:360–365

ABSTRACT: At Murder Creek Research Natural Area, Georgia, USA, we compared structural characteristics of late-successional pine-hardwood stands two to three years after infestation by southern pine beetle (*Dendroctonus frontalis* Zimmerman) to those of adjacent noninfested stands. Death of up to eight *Pinus taeda* L. and *P. echinata* Mill. per mortality patch reduced stem density of pines from 399 to 205 trees ha^{-1}. Stand basal area and average diameter of pines in beetle-infested stands (9.0 m^2 ha^{-1} and 26.9 cm, respectively) were less than those of noninfested stands (30.6 m^2 ha^{-1} and 38.5 cm, respectively). Stand basal area of hardwoods in southern pine beetle-infested stands (9.1 m^2 ha^{-1}) was less than that of noninfested stands (14.5 m^2 ha^{-1}) primarily because of lower abundances of *Liquidambar styraciflua* L. and *Acer barbatum* Michx. However, tree species diversity in beetle-infested stands exceeded that of noninfested stands (Simpson's indices of 0.69 and 0.55, respectively) because proportionate abundance of hardwoods (67% and 33% of total stand basal area, respectively) was increased by the death of pines. Results indicate that small patch mortality from southern pine beetle increased structural complexity of late-successional pine-hardwood stands by causing localized reductions in stem density of large pines (and therefore reduced susceptibility to future beetle attacks) and associated increases in tree species diversity. Development of several old-growth characteristics, particularly increased abundance of snags and dominance by late-successional hardwood species, has been accelerated by southern pine beetle infestation.

Index terms: canopy gap dynamics, *Dendroctonus frontalis, Pinus echinata, Pinus taeda*, tree species diversity

INTRODUCTION

Mixed pine-hardwood forests probably dominated over half of the Georgia Piedmont (USA) prior to European colonization of the early 1800s (Nelson 1957). Following the typical sequence of extensive land clearing, agriculture, erosion, and subsequent land abandonment, loblolly pine (*Pinus taeda* L.) and shortleaf pine (*P. echinata* Mill.) increased dramatically in their abundance throughout the Piedmont (Oosting 1942). These old-field pine stands represent a transition toward a more stable, late-successional forest that includes mixed hardwood species (Peet and Christensen 1987), a process that has been underway in the Georgia Piedmont for the past 80 to 140 years (Brender 1974).

In 1995 southern pine beetle (*Dendroctonus frontalis* Zimmerman) (SPB) proliferated throughout pine forests of the Georgia Piedmont, causing extensive patch mortality (Price et al. 1997). In the Piedmont, SPB typically infests areas of dense pine forest located on heavy clay soils or slopes greater than 10% (Karpinski et al. 1984). High stem density of pine, and therefore close spacing among individual trees, facilitate the spread of SPB (Lorio 1980) and increase the areal growth of pine mortality patches (Turchin et al. 1999). It is believed that susceptibility to SPB attack generally increases with tree age because accumulation of respiring tissue in older trees limits their carbohydrate allocation to synthesis of defensive compounds (Belanger et al. 1993). The presence of hardwoods within a pine stand can confuse migration of SPB and limit their spread (Schowalter and Turchin 1993). However, moderately dense stands of pine are considered high-risk candidates for infestation by SPB if the contribution of hardwood stems to total stand density results in overstocking (Lorio 1994).

In 1997 we initiated a study at Murder Creek Research Natural Area (RNA), Oconee National Forest, to quantify structural characteristics of late-successional pine-hardwood forest two years after the 1995 SPB infestation. We hypothesized that SPB infestation would increase complexity of stand structure by creating gaps in the overstory canopy from death of the larger pines and by shifting tree abundance to a more equitable distribution among pine and hardwood species. Such

dynamics would be important to the long-term management of Murder Creek RNA because they decrease susceptibility of stands to future infestation by SPB (Turchin et al. 1999, Zhang and Zeide 1999), and they accelerate development of several old-growth characteristics (White and White 1996), such as increased abundance of snags and dominance by late-successional hardwood species.

METHODS

Study Area

Murder Creek RNA (33° 17' N, 83° 30' W) of Oconee National Forest is located in Putnam County, central Georgia, approximately 16 km east of Monticello. By 1847 over 99% of Putnam County had been cleared for agriculture (Nelson 1957); however, few additional disturbances have occurred on the RNA for the past 120 years (Saucier et al. 1977). The RNA comprises 449 ha of late-successional forest, including mixed pine-hardwood forest in the uplands and bottomland hardwood forest in the drainages. Upland soils are primarily of the Davidson (Humic Paleudult) and Cecil series (Typic Hapludult) (Long et al. 1922, Saucier et al. 1977). Vegetation of the RNA is classified as the oak-hickory forest type (Oosting 1942, Wharton 1978) with upland forests dominated by canopy (trees > 20 m tall) loblolly and shortleaf pine and subcanopy (trees 12.1–20 m tall) and midstory (trees 6.1–12 m tall) sweetgum (*Liquidambar styraciflua* L.), yellow-poplar (*Liriodendron tulipifera* L.), southern red oak (*Quercus falcata* Michx.), water oak (*Q. nigra* L.), and white oak (*Q. alba* L.). Principal understory (≤ 6 m tall) trees include flowering dogwood (*Cornus florida* L.), Florida maple (*Acer barbatum* Michx.), and American hornbeam (*Carpinus caroliniana* Walt.).

Vegetation Measurements

In May 1997 we located 20 canopy gaps that had originated from recent SPB infestations in upland areas of Murder Creek RNA; essentially every case of recent SPB infestation in the RNA was sampled. Based on previous research (Harrington and Hendrick 1999), we estimated gap age (years) by assuming that SPB-killed pines in two-year-old gaps retain a third or more of their fine branch tips but no needles, while those in three-year-old gaps retain less than a third of their fine branch tips and have sloughing of bark from their boles.

Height of each of five dominant pines surrounding each gap was measured with a clinometer (nearest 0.1 m) and averaged to provide a value for canopy height (H). Maximum length (L) and perpendicular width (W) of each gap were measured as distances between boles of surviving pines (nearest 0.1 m). Gap center was located at the intersection of L and W and permanently marked. Average diameter (D, geometric mean) of each gap was calculated as the square root of L × W. To focus the research on characteristics of discrete canopy openings, we selected gaps having a ratio of average diameter to canopy height (D:H) of 0.3 or greater. Gap area (m^2) was calculated according to the formula for an ellipse, $\pi LW/4$. A non-SPB-infested, pine-hardwood stand located immediately adjacent to each gap was identified for use in paired comparisons of stand characteristics.

To evaluate stand characteristics, we established a circular plot within each SPB-infested stand and noninfested stand that had twice the area of the gap (n = 40 plots in total). This approach minimized bias in estimation of stand-level statistics by providing an equal area in each pair of stands for sampling forest vegetation. Plot area ranged from 93 to 639 m^2 (mean = 237 m^2 ± 33 m^2 SE). Species and dbh (stem diameter in cm at breast height, 1.37 m above ground) were recorded for each living tree of dbh ≥ 2.5 cm rooted within a given plot. Tree species nomenclature follows Little (1979). Dbh of SPB-killed pines was not measured because bark sloughing had occurred on trees in three-year-old gaps, which comprised the majority of the sample.

Statistical Analysis

For each plot, stand basal area ($m^2\ ha^{-1}$), stem density (trees ha^{-1}), and average dbh (cm) were calculated by species and by pine and hardwood categories. Stand basal area was calculated as the total cross-sectional area (πr^2) of trees divided by plot area. Hardwood abundance also was expressed as a proportion of total stand basal area. Average dbh was calculated as the diameter of the tree of mean basal area, which is directly related to stand basal area and stem density (Husch et al. 1982). Given these stand parameters, differences in stand basal area between SPB-infested and noninfested stands were attributed to differences in either average dbh, stem density, or both. Because of missing dbh values for SPB-killed trees, stem density was the only stand parameter that could be evaluated before and after SPB infestation. For each of the pine and hardwood categories, stem density and stand basal area of large trees (dbh ≥ 50 cm) and of small trees (dbh ≤ 10 cm) were calculated for each plot. Stem frequencies of pines and hardwoods were plotted against the midpoint of 5-cm-dbh classes to illustrate variation in stem density with tree size.

We used regression analysis to select an appropriate linear model for describing the relationship of number of tree species to plot area. Combinations of logarithmic and reciprocal transformations were applied to dependent and independent variables, and the model selected for further analysis had highest R^2, lowest mean squared error, and most homogeneous distribution of residuals when plotted against predicted values (Sokal and Rohlf 1981). Regression slopes and intercepts of the selected model were compared (Sokal and Rohlf 1981) between SPB-infested and noninfested stands to identify differences in tree species density (species per unit area; Magurran 1988).

Simpson, Shannon, and evenness indices of tree species diversity were calculated per plot with stand basal area as the measure of tree abundance (Magurran 1988). The Simpson index, a measure of dominance, varies inversely with the probability that any two individuals drawn at random from an infinitely large community will belong to the same species. The Shannon index, a measure of the proportionate abundance of species, is maximal when all species within a community are equally abundant. The evenness index, which varies from 0 to 1, measures the equity with which individuals are distributed among the species present. For comparisons among experimental treatments, the Simpson index is more sensitive than the Shannon index to the one or two most dominant species in a community.

An angular transformation (Sokal and Rohlf 1981) was applied to normalize the proportion of total stand basal area in hardwoods. Each variable, abundance, size, and species diversity of trees, was subjected to a paired *t*-test to detect differences between paired SPB-infested and noninfested stands (Sokal and Rohlf 1981). All analyses were conducted at the 95% significance level (SAS Institute 1989).

RESULTS

Canopy height ranged from 15.7 to 32.4 m (mean = 26.3 m ± 1.1 m SE). Each gap resulted from the death of 1 to 8 pines (44 to 456 trees ha^{-1}, mean = 194 trees ha^{-1} ± 21 trees ha^{-1} SE) and ranged in area from 47 to 319 m^2 (mean = 119 m^2 ± 16 m^2 SE). In general, pines killed by SPB were among the largest trees in each plot. Gap formation was estimated to have occurred either two (2 gaps) or three years (18 gaps) prior to study initiation, corresponding closely to the SPB outbreak of 1995 (Price et al. 1997). Aerial surveys of Putnam County in 1995 indicated that SPB patches (mortality of greater than 5 to 10 trees per group) occurred at densities of 1 to 3 per 405 ha (Price et al. 1997). The D:H ratio of SPB gaps ranged from 0.6 to 1.5 (mean = 0.9 ± 0.06 SE). Such canopy disturbances of low to moderate intensity substantially increase diffuse light but cause only moderate increases in the duration of direct sunlight on the forest floor (Pickett and White 1985).

Stem density of pines prior to SPB infestation was greater in SPB-infested stands (399 trees ha^{-1} ± 84 trees ha^{-1} SE) than in noninfested stands (268 trees ha^{-1} ± 31 trees ha^{-1} SE), although the difference was only marginally significant (*t*-test: $t = 1.76$, df = 19, $P = 0.095$). Higher predisturbance stem densities in SPB-infested stands may have predisposed the pines to SPB attack (Lorio 1980).

Table 1. Mean values of abundance, size, and species diversity of trees (standard error in parentheses) in late-successional pine-hardwood stands two to three years after infestation with southern pine beetle (SPB) versus those of adjacent noninfested stands (n = 20 pairs of stands). Significance levels from the paired *t*-tests (critical $t_{0.05\ [19\ df]}$=2.093) indicate statistical differences.

Variable	SPB-infested stands	Noninfested stands	t	Prob. > t
Tree Abundance				
Pine basal area (m^2/ha)	9.0 (2.2)	30.6 (2.1)	7.54	<0.001
Hardwood basal area (m^2/ha)	9.1 (1.0)	14.5 (1.1)	4.00	0.001
Total basal area (m^2/ha)	18.1 (2.3)	45.1 (2.2)	10.52	<0.001
Pine stem density (trees/ha)	205 (73)	268 (31)	0.97	0.345
Hardwood stem density (trees/ha)	1264 (106)	1623 (103)	2.37	0.029
Total stem density (trees/ha)	1469 (98)	1891 (115)	2.72	0.014
Tree Size				
Pine average dbh (cm)	26.9 (3.3)	38.5 (2.0)	3.73	0.002
Hardwood average dbh (cm)	9.6 (0.5)	10.8 (0.4)	1.88	0.076
Overall average dbh (cm)	12.4 (0.7)	17.7 (0.6)	6.64	<0.001
Tree Species Diversity				
Simpson index	0.69 (0.04)	0.55 (0.03)	2.83	0.011
Shannon index	1.31 (0.08)	1.19 (0.06)	1.33	0.200
Evenness	0.66 (0.03)	0.56 (0.03)	1.88	0.076

Table 2. Mean stand basal area (standard error in parentheses) by tree species in late-successional pine-hardwood stands two to three years after infestation with southern pine beetle versus those of adjacent noninfested stands (n = 20 pairs of stands). Significance levels from the paired *t*-tests (critical $t_{0.05\ [19\ df]}$=2.093) indicate statistical differences.

	Basal Area (m^2/ha)			
Species[a]	SPB-infested Stands	Noninfested Stands	t	Prob. >t
Acer barbatum Michx.	0.42 (0.15)	1.26 (0.35)	2.49	0.022
Acer rubrum L.	0.14 (0.07)	0.30 (0.12)	1.15	0.263
Carpinus caroliniana Walt.	0.35 (0.15)	0.65 (0.22)	1.40	0.179
Cornus florida L.	2.51 (0.55)	3.00 (0.38)	1.07	0.297
Fraxinus americana L.	0.30 (0.22)	0.20 (0.14)	0.65	0.523
Liquidambar styraciflua L.	2.67 (0.44)	4.68 (0.81)	2.13	0.046
Liriodendron tulipifera L.	1.00 (0.42)	1.41 (0.69)	0.55	0.591
Nyssa sylvatica Marsh.	0.19 (0.09)	0.33 (0.12)	0.96	0.347
Ostrya virginiana (Mill.) K. Koch	0.24 (0.11)	0.16 (0.06)	0.64	0.532
Pinus echinata Mill.	0.99 (0.47)	3.55 (1.39)	1.73	0.100
Pinus taeda L.	8.02 (2.16)	27.00 (3.06)	5.36	<0.001
Quercus alba L.	0.28 (0.16)	0.92 (0.46)	1.30	0.210
Quercus falcata Michx.	0.34 (0.22)	0.39 (0.20)	0.17	0.867
Quercus nigra L.	0.32 (0.14)	0.51 (0.15)	0.87	0.398
Ulmus alata Michx.	0.11 (0.07)	0.51 (0.26)	1.45	0.164

[a]Species with 0.1 m^2 ha^{-1} or greater stand basal area.

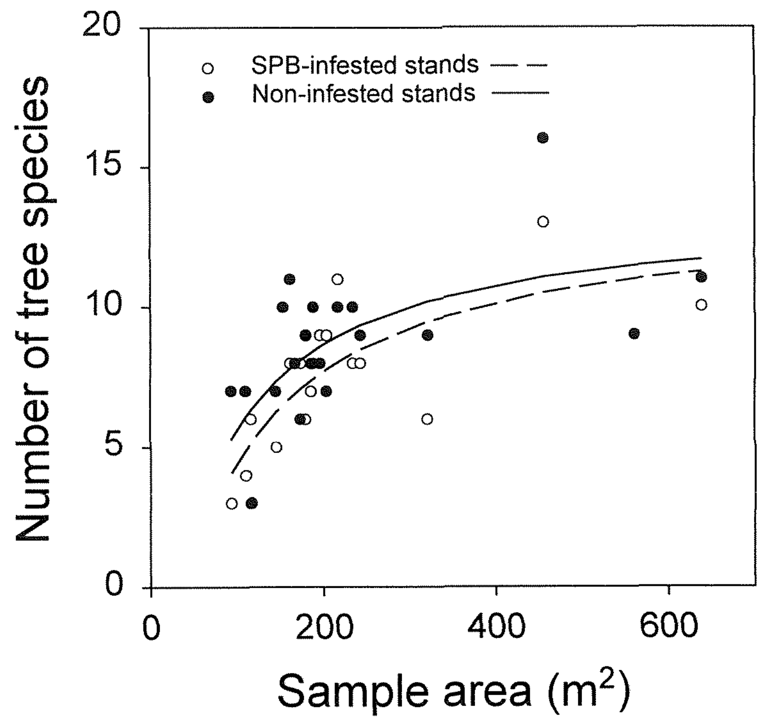

Figure 1. Relationship of number of tree species to plot area in late-successional pine-hardwood stands two to three years after infestation with southern pine beetle (SPB) versus that of adjacent noninfested stands (R^2 = 0.47, overall F = 18.3, P < 0.001, n = 40). Regression model predictions indicate that density of tree species for the mean plot area of 237 m^2 averaged slightly less in SPB-infested stands (8.4) than in noninfested stands (9.2).

Stand basal area of all trees within SPB-infested stands (18.1 m^2 ha^{-1}) averaged only 40% of that observed in non-infested stands (45.1 m^2 ha^{-1}) (Table 1), indicating that SPB greatly reduced the risk rating of these stands for future infestation (Lorio 1980). Because of their high basal area, 68% of which is pine, noninfested stands would be considered high-risk candidates for SPB infestation.

Basal area of pines in SPB-infested stands (9.0 m^2 ha^{-1}) averaged 29% of that observed in adjacent noninfested stands (30.6 m^2 ha^{-1}) (Table 1). These basal area differences can be attributed most to variation in abundance of loblolly, and not shortleaf, pine (Table 2). Average dbh of pines in SPB-infested stands (26.9 cm) was smaller than that of noninfested stands (38.5 cm) (Table 1), suggesting that the larger pines in the stand were those killed by SPB. Stem density of pines did not differ significantly between SPB-infested and noninfested stands (205 and 268 trees ha^{-1}, respectively), indicating that lower values of pine basal area in SPB-infested stands can be attributed to variation in average dbh and not stem density.

Basal area of hardwoods in SPB-infested stands (9.1 m^2 ha^{-1}) averaged 63% of that observed in adjacent noninfested stands (14.5 m^2 ha^{-1}) (Table 1). These basal area differences can be attributed most to variation in abundances of Florida maple and sweetgum (Table 2). Stem density of hardwoods in SPB-infested stands (1264 trees ha^{-1}) averaged 78% of that observed in noninfested stands (1623 trees ha^{-1}), and differences in average dbh were only marginally significant (9.6 vs. 10.8 cm, respectively) (Table 1). Therefore, lower values of hardwood basal area in SPB-infested stands can be attributed more to variation in stem density than to variation in average dbh. Reductions in pine basal area from mortality caused the proportion of total basal area in hardwoods for SPB-infested stands (0.67) to be twice that observed in noninfested stands (0.33).

A total of 22 hardwood species was present in the study area. The following regression model was developed to describe the relationship of number of tree species (N) to plot area (A, m^2):

$$N = e^{2.59-(86.6 + 23.4G)/A}$$

where G = 1 for SPB-infested stands and G = 0 for noninfested stands (Figure 1). In its linear form (R^2 = 0.47, overall F = 18.3, P < 0.001, n = 40), $Ln(N) = b_0 + b_1 (1/A)$, the slope of the regression was somewhat less for SPB-infested stands than for noninfested stands (t-test: t = 1.77, df = 37, P = 0.086), indicating that tree species density was slightly lower in SPB-infested stands. For example, regression predictions for the mean plot area of 237 m^2 indicate values of 8.4 and 9.2 tree species for SPB-infested and noninfested stands, respectively.

The Simpson index of species diversity was greater in SPB-infested stands (0.69) than in noninfested stands (0.55), whereas differences were small to nonsignificant for the evenness and Shannon indices (Table 1). Higher values of the Simpson index for SPB-infested stands resulted from the more equitable distribution of stand basal area among pine and hardwood species following the death of large pines (Table 2).

Frequency distributions for dbh differed markedly between SPB-infested stands and noninfested stands (Figure 2). For example, frequencies of pines of dbh ≥ 25 cm and of hardwoods in most of the dbh classes were lower in SPB-infested than in noninfested stands. SPB-infested stands had lower values for stem density (13 trees ha^{-1}) and basal area (3.3 m^2 ha^{-1}) of large pines (dbh ≥ 50 cm) than those for noninfested stands (58 trees ha^{-1} and 13.9 m^2 ha^{-1}, respectively), presumably a result of tree death from SPB infestation (t-test: $t \geq$ 3.95, df = 19, P<0.001). Both basal area and stem density of small pines (dbh ≤ 10 cm) did not differ significantly between SPB-infested stands and noninfested stands (t-test: $t \leq$ 1.53, df = 19, $P \geq$ 0.14). There were no large hardwoods (dbh ≥ 50 cm) measured in either SPB-infested or noninfested stands. Basal area of small hardwoods in SPB-infested stands (2.5 m^2 ha^{-1}) was lower than that of noninfested stands (3.3 m^2 ha^{-1}) (t-test: t = 2.21, df = 19, P = 0.04), but the difference in stem density of small hardwoods was not significant (t-test: t = 1.03, df = 19, P = 0.32).

DISCUSSION

Results of this study indicate that patch mortality from SPB infestation will increase complexity of stand structure of late-successional pine-hardwood forest in the Georgia Piedmont by causing localized reductions in the density of large pines and, therefore, greater proportionate abundance of hardwoods and diversity of tree species. Although these localized reductions in pine basal area were substantial in this study area, the residual stand still contains pines of various size classes and, hence, retains its late-successional, mixed-species characteristics.

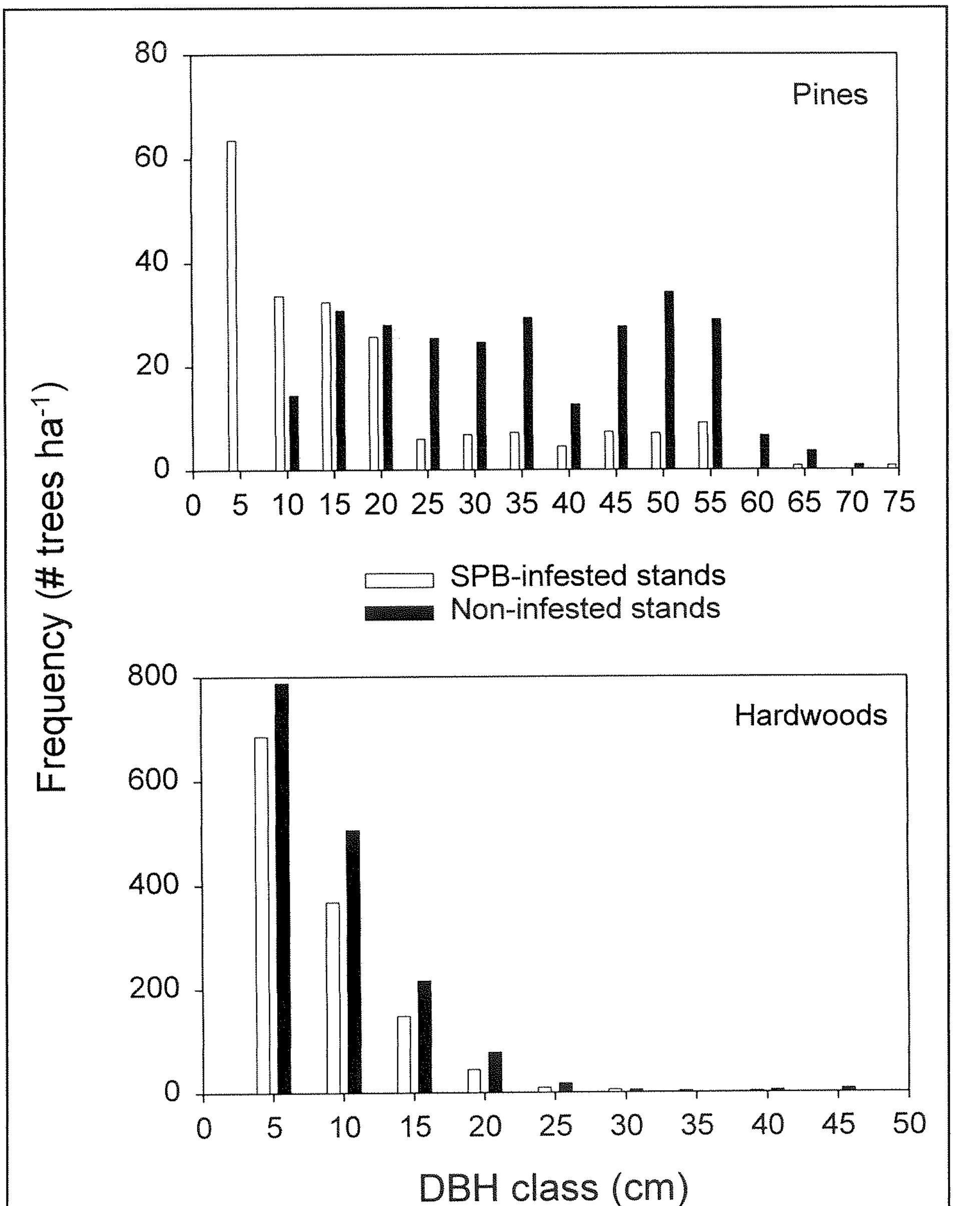

Figure 2. Frequency distributions for stem diameter of pines and hardwoods in late-successional, pine-hardwood stands two to three years after infestation with southern pine beetle (SPB) versus those of adjacent noninfested stands.

Stands infested by SPB had a greater predisturbance stem density of pines, a lower abundance of hardwoods, and a slightly lower density of tree species than those of adjacent noninfested stands. Noninfested stands may have had lower susceptibility to SPB infestation because of their higher stem density of hardwoods. Because they are not a host species for SPB, hardwoods may act as a barrier for beetle dispersal to adjacent pines (Schowalter and Turchin 1993). In addition, foliage of specific hardwoods (e.g., sweetgum) emits volatile compounds that confuse the ability of SPB to locate other pine trees (Dickens et al. 1992). However, the retrospective nature of this study precludes identification of the exact role that hardwoods played in suppressing SPB infestation in noninfested stands.

Given the new growing space resulting from patch mortality, we expect that hardwoods will become increasingly dominant in SPB-infested stands. Because the disturbance was of sufficient intensity to stimulate understory reinitiation (Oliver and Larson 1996), increases in hardwood dominance will result from both increased growth of existing trees and initiation of new stems. Of the existing trees, species of greatest initial size or abundance are likely to benefit most, specifically yellow-poplar, sweetgum, and flowering dogwood. In response to increases in availability of diffuse light, new stems are likely to be initiated by species of medium to high shade tolerances, including white oak, southern red oak, Florida maple, American hornbeam, and eastern hophornbeam (Burns and Honkala 1990).

These canopy gap dynamics should reduce overall susceptibility of the forest to SPB infestation because spacing among residual pines has been increased and the larger pines have been reduced in abundance. In addition, SPB infestation has accelerated development of several old-growth characteristics, particularly increased abundance of snags and dominance by late-successional hardwood species. Although once heavily dominated by pine, SPB-infested stands now have similar abundances of pines and hardwoods. As a patchwork of scattered small-gap disturbances, SPB infestations are accelerating the transition of old-field, pine-hardwood forest at Murder Creek RNA toward a steady-state forest ecosystem and recovery from decades of tillage farming.

ACKNOWLEDGMENTS

Financial support for this research was provided by the USDA Forest Service, Southern Research Station and the McIntire-Stennis Program (Project GEO-0067-MS). The authors are grateful to W.E. O'Connell and M.D. Yates for their assistance with field measurements and to two anonymous reviewers for constructive comments on the manuscript.

Tim Harrington, Associate Professor of Silviculture and Applied Ecology, conducts research and teaches classes on forest stand dynamics of southern pine and Douglas-fir ecosystems.

Mingguang Xu is a Statistician for the University System of Georgia.

Boyd Edwards is a Research Ecologist with professional interests in ecosystem restoration and applied ecology.

LITERATURE CITED

Belanger, R.P., R.L. Hedden, and P.L. Lorio Jr. 1993. Management strategies to reduce losses from southern pine beetle. Southern Journal of Applied Forestry 17:150-154.

Brender, E.V. 1974. Impact of past land use on the lower Piedmont forest. Journal of Forestry 72:34-36.

Burns, R.M. and Honkala, B.H. (eds.). 1990. Silvics of North America, Vol. 2, Hardwoods. Agriculture Handbook No. 654, U.S. Department of Agriculture, Forest Service, Washington, D.C. 877 pp.

Dickens, J.C., R.F. Billings, and T.L. Payne. 1992. Green leaf volatiles interrupt aggregation pheromone response in bark beetles infesting southern pines. Experientia 48:523-524.

Harrington, T.B. and R.L. Hendrick. 1999. Tree growth and resource availability in response to simulated canopy gaps in mature slash pine forest. Pp. 374-376 *in* J.D. Haywood, ed., Proceedings of the Tenth Biennial Southern Silvicultural Research Conference. General Technical Report SRS-30, U.S. Department of Agriculture, Forest Service, Asheville, N.C. 618 pp.

Husch, B., C.I. Miller, and T.W. Beers. 1982. Forest Mensuration. 3rd Ed. John Wiley and Sons, New York. 402 pp.

Karpinski, C., Jr., R.L. Hedden, R.P. Belanger, and T.S. Price. 1984. Guidelines for managing pine bark beetles in Georgia. Publication 235-1, Georgia Forestry Commission, Macon. 61 pp.

Little, E.L., Jr. 1979. Checklist of United States Trees (Native and Naturalized). Agriculture Handbook 541, U.S. Department of Agriculture, Forest Service, Washington, D.C. 375 pp.

Long, D.D., E.T. Maxon, N.M. Kirk, H.G. Lewis, F.A. Hayes, E.C. Hall, H.V. Geib, and G.A. Crabb. 1922. Soil survey of Oconee, Morgan, Greene and Putnam Counties, Georgia. U.S. Department of Agriculture, Bureau of Soils. 61 pp.

Lorio, P.L., Jr. 1980. Loblolly pine stocking levels affect potential for southern pine beetle infestation. Southern Journal of Applied Forestry 4:162-165.

Lorio, P.L., Jr. 1994. Southern pine beetle risk ratings. Pp. 162-171 *in* Proceedings of the Symposium on Ecosystem Management Research in the Ouachita Mountains: pretreatment conditions and preliminary findings. General Technical Report SO-112, U.S. Department of Agriculture, Forest Service, New Orleans, La. 259 pp.

Magurran, A.E. 1988. Ecological Diversity and Its Measurement. Princeton University Press, Princeton, New Jersey. 179 pp.

Nelson, T.C. 1957. The original forests of the Georgia Piedmont. Ecology 38:390-397.

Oliver, C.D. and B.C. Larson. 1996. Forest Stand Dynamics. Update Ed. John Wiley and Sons, New York. 520 pp.

Oosting, H.J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. American Midland Naturalist 28:1-126.

Peet, R.K. and N.L. Christensen. 1987. Competition and tree death. BioScience 37:586-595.

Pickett, S.T.A. and P.S. White (eds.). 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York. 472 pp.

Price, T.S., C. Doggett, J.M. Pye, and B. Smith. 1997. A history of southern pine beetle outbreaks in the southeastern United States. Southeastern Forest Insect Working Group, Georgia Forestry Commission, Macon. 72 pp.

SAS Institute. 1989. SAS/STAT User's Guide. Version 6, 4th Ed., Vol. 2. SAS Institute Inc., Cary, N.C. 1686 pp.

Saucier, J.R., A.P. Durkas, J.W. Moore, and R.L. Hendricks. 1977. Murder Creek Research Natural Area. Establishment Report, U.S. Department of Agriculture, Forest Service, Southern Region, Atlanta, Ga. 15 pp.

Schowalter, T.D. and P. Turchin. 1993. Southern pine beetle infestation development: interaction between pine and hardwood basal areas. Forest Science 39:201-210.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. 2nd Ed. W.H. Freeman and Co., New York. 859 pp.

Turchin, P., J. Davidson, and J.L. Hayes. 1999. Effects of thinning on development of southern pine beetle infestations in old growth stands. Southern Journal of Applied Forestry 23:193-196.

Wharton, C.H. 1978. The Natural Environments of Georgia. Georgia Department of Natural Resources, Atlanta. 227 pp.

White, P.S. and R.D. White. 1996. Old-growth oak and oak hickory forests. Pp. 178-198 *in* M.B. Davis, ed., Eastern Old-Growth Forest: Prospects for Rediscovery and Recovery. Island Press, Washington, D.C. 383 pp.

Zhang, Y. and B. Zeide. 1999. Which trees and stands are attacked by southern pine beetle? Southern Journal of Applied Forestry 23:217-223.