CASTANEA 68(3): 211–221. SEPTEMBER 2003

Structural Characteristics of Frequently-Burned Old-Growth Longleaf Pine Stands in the Mountains of Alabama

J. MORGAN VARNER, III,* JOHN S. KUSH, and RALPH S. MELDAHL

School of Forestry and Wildlife Sciences, 108 M.W. Smith Hall,
Auburn University, Alabama 36849-5418

ABSTRACT

Age and structural characteristics were measured in two frequently burned old-growth mountain longleaf pine (*Pinus palustris* Mill.) communities along Choccolocco Mountain in northeastern Alabama. Stands studied were open-canopied and park-like (8.3 to 13 m^2 ha^{-1} basal area; 282–297 trees ha^{-1}), fitting historical descriptions of the now endangered communities. Maximum pine ages in the two stands exceeded 240 years. Both stands underwent continuous pine recruitment over the past 145 years, with all 5-year age classes represented. Congregations of even-aged pine patches were found throughout both stands. Multiple tree patches ranged from 15 to 170 years old. Large even-aged patches were present in both stands (up to 2124 m^2), though isolated single trees were more common, accounting for about half of all patches. Continued work on pristine remnant forests and savannas is necessary due to their increasing rarity and importance as reference models for management and restoration.

INTRODUCTION

Age and stand structure of forested ecosystems are necessary components for both understanding their natural history and management. Age structure (the organization of forests in space and time) gives information on past disturbances (e.g., Cooper 1960, Lorimer 1980, Foster 1988) and replacement processes of ecosystems. Stand structure studies (spatial distribution of trees within a forested stand) generally describe present conditions and their implications for future growth (Covington and Moore 1994), as guides to forest management (Lindenmayer and Franklin 1997, Palik et al. 1997, Noel et al. 1998), or as descriptive models for understanding forest stand dynamics (Oliver and Larson 1990, Palik and Pederson 1996).

Longleaf pine forests and savannas of the southeastern United States have been the subject of several forest structure studies. Age structure has been well-studied in Coastal Plain longleaf pine stands (Schwarz 1907, Chapman 1909, Forbes 1930, Platt et al. 1988, Platt and Rathbun 1993, Meldahl et al. 1999). Stand structure has been studied more extensively (Reed 1905; Schwarz 1907; Chapman 1909, 1923; Forbes 1930; Wahlenberg 1946; Platt et al. 1988; Meldahl et al. 1999). Our understanding of longleaf pine forest structure and dynamics is derived from studies of natural disturbance (Schwarz 1907, Boyer 1979, Platt et al. 1988, Platt and Rathbun 1993, Palik and Pederson 1996), the even-aged patches they create (Platt et al. 1988, Platt and Rathbun 1993), and their legacy on stand structure at the stand and landscape level (Platt et al. 1988). Applying this understanding of structure, forest managers can manipulate the size, shape, and timing of harvested openings (gaps) to closely resemble gaps in natural forests, encourage establishment and/or create patchy forests (Neel 1971, Palik et al. 1997, Noel et al. 1998).

Early investigators concluded that primary longleaf pine-dominated forests and savannas were open-canopied, pure, and uneven-aged (Reed 1905, Schwarz 1907, Chapman 1909,

* Present address: College of Natural Resources, University of Florida, Box 118526, Gainesville, Florida 32611-8526. email address: jmvarner@botany.ufl.edu

Wahlenberg 1946). This uneven-aged community consisted of variably sized, even-aged patches. These patches were the result of recruitment into openings created by windstorms, hot fires, and insect-induced mortality (Schwarz 1907, Chapman 1909, Wahlenberg 1946). Patches ranged from 0.04 to 0.2 ha (Schwarz 1907, Chapman 1909), with occasional 1,000 to 3,000 m strips created by tornadoes and hurricanes (Reed 1905, Wahlenberg 1946). The overstory of virgin longleaf pine forests consisted of individual trees with diameters up to 100 cm, and heights up to 40 m (Reed 1905, Chapman 1909). Basal area ranged from 12 to 35 m^2 ha^{-1} (Reed 1905, Schwarz 1907). Stand density ranged from 130 to 400 trees ha^{-1}; snag density averaged 15 snags ha^{-1} (Reed 1905, Schwarz 1907).

Open, park-like forests dominated by longleaf pine once blanketed over 37 million ha of the southeastern United States (Ware et al. 1993). These pinelands have wide ecological amplitude, once dominating landscapes over a broad array of physiographic, climatic, and edaphic conditions (Sargent 1884, Mohr 1897, Wahlenberg 1946, Craul 1965). Since European settlement, longleaf pine forest acreage has plummeted to less than 3% of its former range, numbering fewer than 1.2 million ha (Outcalt and Sheffield 1996), making longleaf pinelands among the most endangered ecosystems in the United States (Noss et al. 1995). Further, most remnant communities lack ecological integrity (Ware et al. 1993, Outcalt 2000) and less than 0.01% remains as old-growth (Means 1996, Varner and Kush 2001).

In comparison to the body of literature that exists on Coastal Plain longleaf pine forests, the mountain longleaf pine forest is poorly understood. The mountain (or montane) longleaf pinelands are located in the Piedmont, Ridge and Valley, Cumberland Plateau, and Blue Ridge physiographic provinces of Alabama and Georgia. The literature is confined to old reports and descriptions (Mohr 1897; Reed 1905; Harper 1905, 1913, 1928, 1943; Andrews 1917), with few contemporary additions. Mohr (1897) and Reed (1905) described the virgin mountain pinelands as pure pine forests of large diameter (averaging 60–63 cm DBH, with individuals exceeding 100 cm) and great heights (exceeding 35 m). Reed (1905) described a large tract of old-growth mountain longleaf pine forest in Coosa County in north central Alabama. At that time, "longleaf pine land" occupied 87% of the landscape, with "creek land" occupying the remainder. Another primary shortcoming in all pineland structure studies is the lack of integration over space and time (but see Platt and Rathbun 1993). Finally, recent ecosystem management recommendations (Palik et al. 1997, Brockway and Outcalt 1998, Noel et al. 1998) have been based on secondary forests, a small number of stands, short time scales, and most importantly only Coastal Plain sites. There is need for more work from old-growth stands, particularly from outside of the Coastal Plain.

To address these shortcomings, we initiated this study in 1998 at Fort McClellan, a United States Army garrison containing the finest remaining mountain longleaf pinelands. The objectives of this study were to 1) describe the age and stand structure, 2) evaluate the size, age, and variability in even-aged patches, and 3) shed light on past disturbance and replacement patterns of two remnant old-growth mountain longleaf pine stands. This project was initiated to inform managers of regional forests, to describe benchmark conditions for regional restoration efforts, and to aid our overall understanding of forest stand dynamics.

STUDY AREA AND METHODS

Our study area was located within Fort McClellan, a 7,300 ha United States Department of Defense Army Garrison in eastern Calhoun County, Alabama (33°42′N, 85°45′W; Figure 1). Fort McClellan contains a large segment of Choccolocco Mountain and its spur ridges, all capped with Weisner quartzite. Climate is warm and humid, with mean annual temperature 17°C. Winters are short and mild; summers are long, humid, and warm. Precipitation is evenly distributed throughout the year with small peaks associated with summer thunderstorm events and troughs occurring during October. Annual precipitation averages 1,250 mm, with small amounts falling as ice and snow (Harlin et al. 1961, Craul 1965).

Since 1994, surveys at Fort McClellan identified twelve old-growth longleaf pine stands (Varner 2000). For the purposes of this study, "old-growth" was defined as those stands

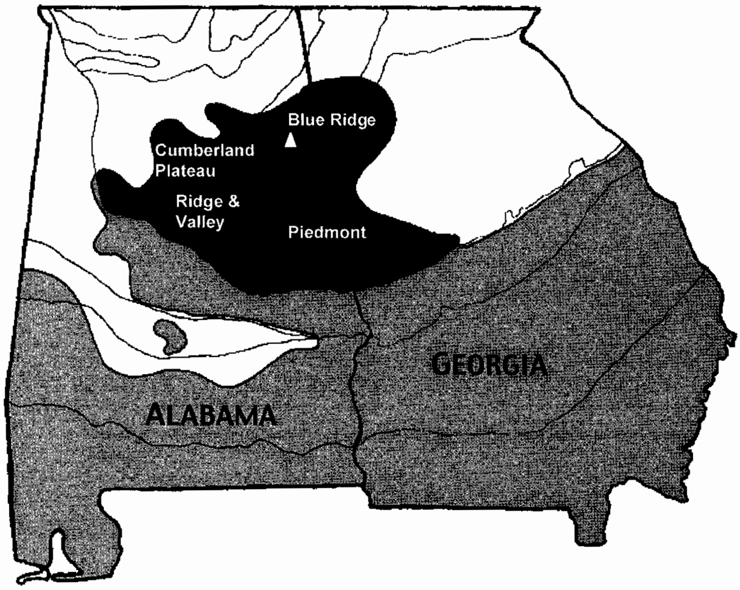

Figure 1. Native range of longleaf pine in Alabama and Georgia (light and dark shaded areas). Dark shaded region denotes the range of mountain longleaf pine-dominated forests and savannas. Physiographic provinces represented by this region are in white type. The white triangle represents the approximate location of our study site, Fort McClellan.

containing age classes (not individual trees) predating settlement. At Fort McClellan, settlement did not occur until ca. 1850 or later (Reed et al. 1994). Two old-growth stands were selected with frequent burning histories (1 to 3 year return interval) and good accessibility during military training (avoiding frequently closed areas). The two stands, hereafter referred to as Caffey Hill and Red-tail Ridge, were located at ca. 450 and 350 m above mean sea level. Caffey Hill is an upper slope stand covering 1.5 ha abutting a 250 ha matrix of younger stands downslope. Red-tail Ridge spans a mid- to upper slope position covering 1.8 ha abutting a fire-excluded 20 ha tract down- and side slope. Soils were mapped as Rough Stony Land-Sandstone, with intergrades of Anniston soils. Rough Stony Land-Sandstone is a miscellaneous soil type that represents soils with many outcrops of quartzite and sandstone bedrock, loose rock fragments, and scattered patches of shallow sandy soil (Harlin et al. 1961). Anniston soils are clayey, kaolinitic, thermic Rhodic Paleudults with surficial loams, transitioning to clay-loams in subsoils (Harlin et al. 1961). Slopes of the two sites ranged from 40 to 60% at Caffey Hill and 30 to 45% at Red-tail Ridge. Caffey Hill had a SSE aspect, while Red-tail Ridge's aspect was WSW, both typical of Fort McClellan and other mountain longleaf pinelands (Varner 2000).

Within each stand, we measured all living longleaf pines >2.5 cm DBH (100% sample) for DBH (to nearest 0.25 cm), crown and total height (to nearest m), and distance and direction from permanent plot centers (located for concurrent study on groundcover; see Varner et al. 2003) to create stand maps to delineate patch structure (see below). All snags were measured for DBH, total height, and distance and direction from permanent plot centers.

All living pines >10 cm DBH were cored at 1 m above the root collar (stems <10 cm were avoided to minimize coring-induced mortality). All cores were dried for >48 hr, mounted and glued on wooden mounts, and sanded (with progressively finer textures, terminating with 400 grit sandpaper) for microscope examination to determine ring count. Since longleaf pine does not produce annual growth rings during its juvenile grass stage, true age cannot be determined (Pessin 1934). Ring count at 1 m was used as a surrogate (although an underestimate) for age, as has been done in previous studies (Platt et al. 1988, Meldahl et al. 1999). Age class distributions were plotted using five-year age classes, due to frequent masts observed in

Table 1. Age and structural characteristics of old-growth longleaf pine stands at Fort McClellan, Alabama (Caffey Hill and Red-tail Ridge), compared with other published old-growth longleaf pine stands

	Stand			
Character	Caffey Hill	Red-tail Ridge	Coastal Plain Old-growth[1]	Coosa Tract[2]
Stem density (trees ha^{-1})	298	283	36–395	131–205
Snag density (trees ha^{-1})	8.6	11.1	15–18	N/A
Basal area (m^2 ha^{-1})	8.3	13.0	15–35	11–13
Arithmetic mean DBH (cm)	14.7	20.3	25.1–?	26.4–?
Maximum DBH (cm)	55.0	70.5	81.5–100+	106.5
Mean total height (m)	7.9	12.4	17–?	N/A
Max total height (m)	19.8	27.1	33.5–40+	33.8
Mean live crown (%)	52.0	44.5	46–?	N/A
Maximum age (rings @ 1 m)	228+	238	280–450+	N/A
Mean age (trees >10 cm DBH)	64.8	61.9	55.7–?	N/A
Redheart decay incidence[3]	5.3	3.6	1.8–2.2	N/A

[1] Coastal plain old-growth data are taken from Schwarz 1907, Platt et al. 1988, and Meldahl et al. 1999.
[2] Coosa Tract old-growth data are taken from Reed 1905.
[3] Decay for all sites based on visual evidence of rotten heartwood at 1 m, so all are underestimates by the same methodology.

mountain longleaf pine stands (Boyer 1987). All extracted cores were visually examined for presence of heartwood decay, indicating redheart disease [caused by the fungus *Phellinus (Fomes) pini* (Brot.) Ames]. Trees may be infected with the fungus, but not exhibit decay where cored. Decay values, therefore, were underestimates of actual decay but allow for comparison with similarly analyzed longleaf pine stands (Platt et al. 1988, Meldahl et al. 1999).

Maps of all longleaf pine stems were plotted to delineate and measure even-aged patches. Patches were defined as spatially and temporally discrete aggregations of trees. Lone individuals were also treated as "patches" if they differed in age or were a great distance from similarly aged individuals. To differentiate patches, we used cluster analysis (PROC CLUS; SAS Institute 1990); using the variables: X-distance, Y-distance, and tree age (Z). This analysis, however, decreased the value of age in the even-aged patch clustering. To increase the importance of age, we squared all age values for our cluster analyses. This technique separated young trees conservatively (their ages could be determined more easily and they tended to be conglomerated), and clustered old trees (which would have more missing rings and have undergone greater mortality with time). Squaring age (Z^2) kept within-patch age ranges low (Red-tail Ridge max range = 13 years; Caffey Hill max range = 12 years).

We measured patch sizes by manually overlaying plotted patch maps with 6 × 6 m pixels (a good approximation for crown size of open-grown longleaf pines; Kush et al. 1989). Counts of pixels occupied by each patch (to better identify patches, not just individuals) were tallied and summed for estimates of patch extent.

RESULTS

While minor structural differences existed between the two stands, most structural variables were somewhat similar (Table 1). Differences were most pronounced in basal area and tree DBH. Stand density was similar to values derived from both historical (Schwarz 1907) and contemporary (Platt et al. 1988, Meldahl et al. 1999) Coastal Plain old-growth stand measurements. Both Caffey Hill and Red-tail Ridge had higher tree densities than prior mountain descriptions (Reed 1905). Basal area, tree DBH, and snag density were all much lower than values derived from Coastal Plain old-growth stands. These differences are not so pronounced when compared with historical mountain descriptions (Reed 1905), with basal area

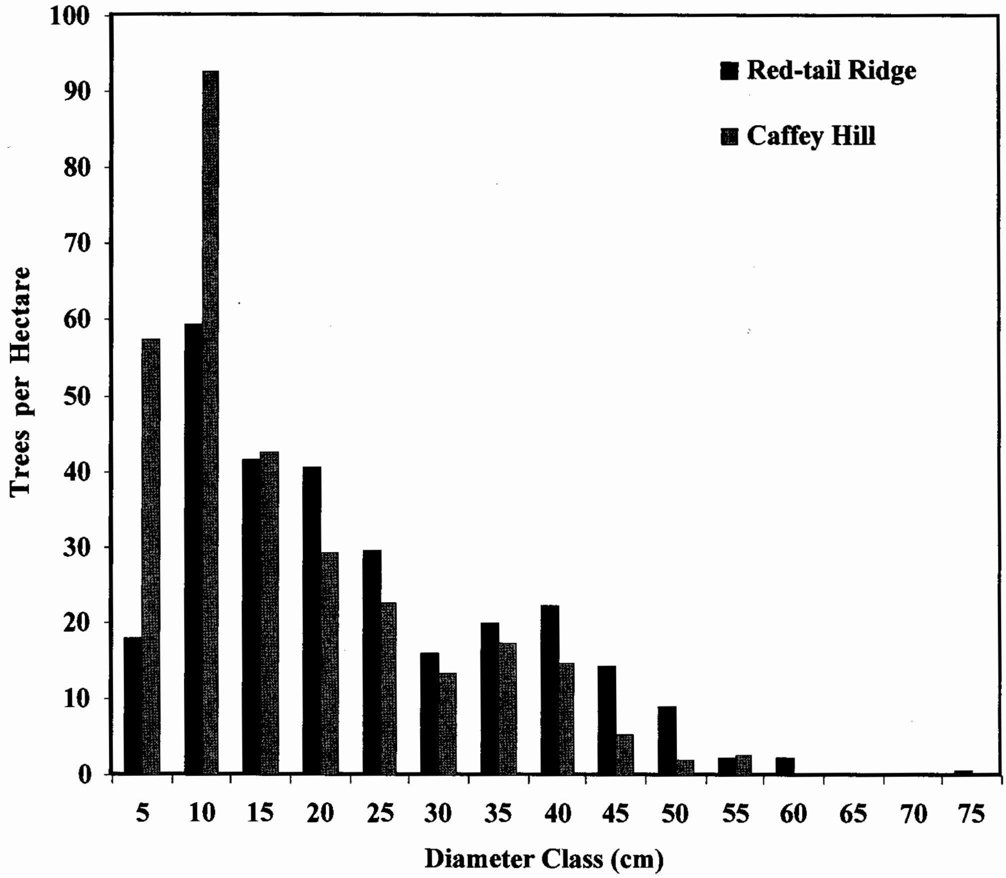

Figure 2. Stand structure of Caffey Hill and Red-tail Ridge, two frequently burned old-growth mountain longleaf pine stands at Fort McClellan, Alabama.

and mean DBH being somewhat similar. Maximum heights and DBH for both Coastal Plain and prior mountain descriptions were markedly larger than either Caffey Hill or Red-tail Ridge.

Both stands mimic the wave-like reverse-j shaped curves found in previous studies of old-growth longleaf pine forests (Figure 2; Reed 1905, Schwarz 1907, Platt et al. 1988, Meldahl et al. 1999). These two stands differ from previously described stands by lacking large individuals, lacking sufficient representation in the larger diameter classes (above 50 cm) and small maximum heights (<25 m). Snag densities in both stands were less than previous reports of 15 to 18 ha^{-1} in Coastal Plain old-growth longleaf pine forests (Schwarz 1907, J.S. Kush, unpubl. data). Differences are pronounced when both stands' diameter distributions are plotted (Figure 2). Both stands have peaks in the 10 to 20 cm and 35 to 40 cm diameter classes. Troughs differ, with Caffey Hill having a major trough in the 30 cm and above 40 cm diameter classes, while Red-tail Ridge has troughs in the smaller (below 10 cm) and in the 30 and above 50 cm diameter classes.

Within Caffey Hill, 191 trees were cored and aged. Ring counts of trees ranged from 12 to 228+ years (Table 1). The two oldest individuals at Caffey Hill both contained decayed heartwood, so stand maximum ages exceeded these values. At Red-tail Ridge, 352 trees were cored and aged. Ring counts of trees ranged from 12 to 238 years.

The two old-growth stands had different age structures (Figure 3). Several distinct age classes were found in each stand. Sharp peaks were found in the 25 to 40, 45 to 60, and 115 to

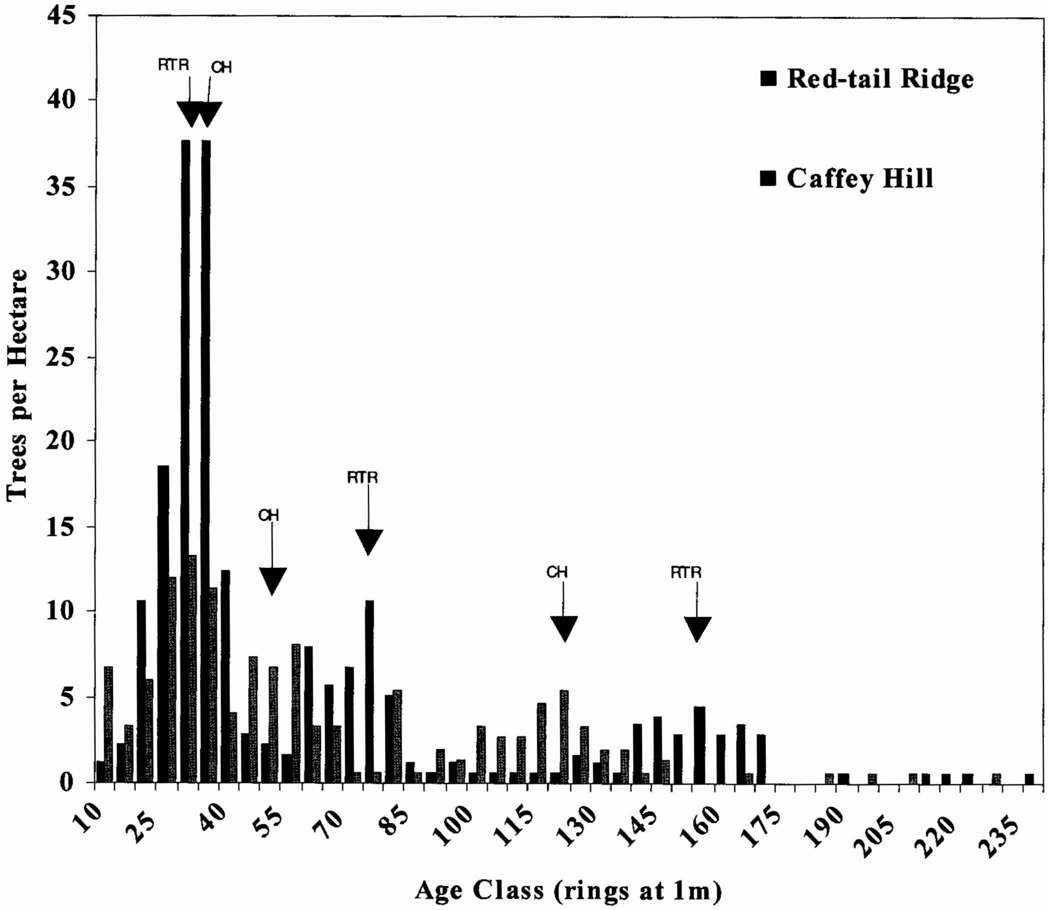

Figure 3. Age structure of two old-growth mountain longleaf pine stands at Fort McClellan, Alabama. Arrows indicate age class peaks in each stand (RTR = Red-tail Ridge; CH = Caffey Hill).

130 year age classes at Caffey Hill. Peaks in the 20 to 45, 60 to 85, and 145 to 175 year age classes were present at Red-tail Ridge. Corresponding peaks between the two stands were found only in the 25 to 40 year age classes. All age classes between 10 and 145 years were represented, indicating nearly continuous recruitment in the two stands for more than a century.

Both stands contained numerous even-aged patches (Figure 4), averaging 43.3 and 52.7 patches ha^{-1} at Red-tail Ridge and Caffey Hill, respectively. Mean patch sizes were 2.8 trees $patch^{-1}$ at Caffey Hill and 4.5 trees $patch^{-1}$ at Red-tail Ridge (Table 2). Patch boundaries overlapped each other, and many contained older or younger aged patches within their boundaries. Mean patch creation rates at Caffey Hill were 2.1 patches ha^{-1} 10 yr^{-1}, and at Red-tail ridge 1.7 patches ha^{-1} 10 yr^{-1} (Table 2). Patch sizes ranged from single trees (44 to 51% of all patches at the two sites) to large, irregularly elliptic patches with up to 77 individuals (Red-tail Ridge's 40 year old patch). Patch sizes ranged to 612 m^2 at Caffey Hill, and to 2124 m^2 at Red-tail Ridge. Large (>10 trees) patches at Caffey Hill were found in the 30, 40, 55, 80, 125 and 130 year age classes. Each of these patches was visible at the stand level age class distribution (Figures 3 and 4), except the 130 year patch. Absent from patches was representation from the 25–45, and 60 year age classes. Patches at Red-tail Ridge were larger and more uniform. Large (>10 trees) patches at Red-tail Ridge were found in the 35, 40, 45, 75 and 170 year age classes. All six large patches at Red-tail Ridge correspond to stand-level age class distribution (Figures 3 and 4).

Table 2. Patch characteristics of two old-growth mountain longleaf pine stands at Fort McClellan, Alabama

Character	Stand	
	Caffey Hill	Red-tail Ridge
Patches ha^{-1}	52.7	43.3
Patch creation rate (patches ha^{-1} 10 yr^{-1})[1]	2.1	1.7
Single tree patches (%)	44.3	52.6
Max patch size		
Trees per patch (age)	20 (15)	45 (45)
Area (m^2)	612	2124
Mean patch size		
Trees per patch (s.d.)	2.8 (3.5)	4.5 (8.5)
Area (m^2)	91.3	173.5
Total number of patches	79	78
No. patches >10 trees (ha^{-1})	6 (4.0)	6 (3.3)
No. patches >25 trees (ha^{-1})	1 (0.7)	5 (2.8)

[1] Patch creation rate was calculated where: Patch creation rate = (# of patches ha^{-1}/max stand age) * 10 years, where maximum stand age is set at 250, a good approximation of both stands' maximum age. Using our clustering methodology, within-patch age range was low, 12 years for Caffey Hill and 13 years for Red-tail Ridge.

Fort McClellan's 12 old-growth stands (Varner 2000)] exceed rates of decay reported in other old-growth longleaf pine forests (cf. Platt et al. 1988, Meldahl et al. 1999). Decayed heartwood may sufficiently weaken trees enough to increase ice and wind mortality (Varner 2000).

Disturbance in mountain longleaf pine forests is poorly understood. Coastal Plain longleaf pine forests are proximal to coastal storms, and thus have high probabilities of experiencing hurricanes, tornadoes, and other wind disturbances (Schwarz 1907, Wahlenberg 1946, Platt and Rathbun 1993). Conversely, mountain longleaf pine forests are located at the maximal distance from coastal storms (Fort McClellan is ca. 400 km from the Gulf of Mexico), though occasional hurricanes and downbursts do penetrate into the southern Appalachians (Greenberg and McNab 1998). While gaps are being created frequently in mountain stands (approx. 2 patches originate ha^{-1} $decade^{-1}$; Table 2), their origin is perplexing. Lipps (1966) cited ice storm disturbance as a major mortality agent in mountain longleaf pine stands in north Georgia (Lavender Mountain, Floyd County). Ice storms alone, however, do not explain structure and composition of mountain longleaf pine stands, since ice storms tend to encourage dominance by invading hardwood species in the southern Appalachians (Rhoades 1999). Also, windstorms from Gulf Coastal storms do induce significant damage in forests even farther inland than these mountain stands (Greenberg and McNab 1998). Ice, in concert with wood decaying fungus [particularly *Phellinus* (*Fomes*) *pini* (Brot.) Ames] and subsequent wind or ice storms, may be influential to stand dynamics and structural characteristics of mountain pinelands (Varner 2000). Disturbance factors, their importance, occurrence, and magnitude are neglected topics in understanding mountain longleaf pine forest ecology and dynamics.

Red-tail Ridge's larger and more variable patches (Table 2) and stronger relationship between age class peaks and patches (Figures 3 and 4) suggests that it has a history of large-scale disturbances (multiple tree mortality). The size and distribution of patches at Red-tail Ridge may be the result of past lumbering or other large catastrophic disturbance (fire, ice, or wind). Age class peaks combined with both large and small patch representation found across stands increase the probability of a past large-scale regeneration event. Stand-level peaks may also be indicative of such a situation, but may be indicators of more localized disturbances. Dendrochronological analysis to determine stand history (e.g., Lorimer 1980) may explain the disparities between these two stands. Indeed, analysis of patch size, distribution, and dynamics should be a high priority for all remaining old-growth longleaf pine stands.

The most provocative findings were related to patch structure—patch size, age, and heterogeneity. Single tree "patches" were numerous (Table 2 and Figure 4), surprisingly dominant in an ecosystem assumed to be comprised of multiple individual patches. This assumption has historically hampered the application of single-tree selection regeneration practices to longleaf pine forests. Large patches (>10 trees) were conspicuous at both sites, and several predated European settlement. This fact is strengthened by the large size of two older, presettlement patches at Red-tail Ridge (150 and 170 year old patches). Reed (1905) suggested that patch sizes were large and common in mountain longleaf pine forests. Our results at Fort McClellan suggest that single-tree selection in concert with a group selection system may be a better mimic to natural longleaf pine stand dynamics than group selection systems alone. Further sampling and experimentation are warranted.

Frequently burned pinelands are increasingly rare in the contemporary southeastern mountain landscape (Varner et al. 2003); old-growth forests and savannas are even further imperiled. Before they are extinct, we must understand stand dynamics—including disturbance factors, replacement processes, and persistence. With this understanding, scientists and forest managers can more holistically restore and manage southern pinelands and their diverse habitats.

ACKNOWLEDGMENTS

We thank R. Sampson, C. Avery, M. Earle, B. Lindsey, E. Reynolds, S. Harrison, and D. Shaw for their field and laboratory assistance. Discussions with W. Boyer, D. Folkerts, M. MacKenzie, and reviews by K. Outcalt and an anonymous reviewer greatly enhanced the quality of this manuscript. The assistance provided by Directorate of Environment personnel, especially R. Smith and B. Garland, was invaluable. Funding was provided by a United States Department of Defense Legacy Fund, Cooperative Agreement No. USFS-SRS-33-CA-97019 and the Auburn University School of Forestry and Wildlife Sciences.

LITERATURE CITED

Andrews, E.F. 1917. Agency of fire in propagation of longleaf pines. Bot. Gaz. 64:497–508.

Boyer, W.D. 1979. Mortality among seed trees in longleaf pine shelterwood stands. South. J. Appl. Forest. 3:165–167.

Boyer, W.D. 1987. Annual and geographic variations in cone production by longleaf pine. p. 73–76. *In*: Phillips, D.R. (ed.). Proceedings of the 4th Biennial Southern Silvicultural Research Conference. USDA Forest Service, Southern Forest Experiment Station, Gen. Tech. Rep. SE-42, Asheville, North Carolina.

Boyer, W.D. 1990. *Pinus palustris* Mill. longleaf pine. p. 405–412. *In:* Burns, R.M. and B.H. Honkala (Tech. Coords.). Silvics of North America. Volume 1. Conifers. USDA Forest Service, Washington, D.C.

Brockway, D.G. and K.W. Outcalt. 1998. Gap-phase regeneration in longleaf pine wiregrass ecosystems. Forest Ecol. Manage. 106:125–139.

Chapman, H.H. 1909. An experiment in logging longleaf pine. For. Quarterly 7:385–395.

Chapman, H.H. 1923. The cause and rate of decadence in stands of virgin longleaf pine. Lumber Trade J. 84:11,16–17.

Cooper, C.F. 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. Ecol. Monogr. 30:129–164.

Covington, W.W. and M.M. Moore. 1994. Southwestern ponderosa pine forest structure: changes since Euro-American settlement. J. Forest. 92:39–47.

Craul, P.J. 1965. Longleaf pine site zones. Final Report FS-SO-1103. USDA Forest Service, Southern Research Station, Auburn, Alabama.

Forbes, R.D. 1930. Timber growing and logging and turpentining practices in the southern pine region. USDA Forest Service, Techn. Bull. 204, Washington, D.C.

Foster, D.R. 1988. Disturbance history, community organization and vegetation dynamics of the old growth Pisgah Forest, southwestern New Hampshire USA. J. Ecol. 76:105–134.

Greenberg, C.H. and W.H. McNab. 1998. Forest disturbance in hurricane-related downbursts in the Appalachian mountains of North Carolina. For. Ecol. Manage. 104:179–191.

HARLIN, W.V., H.T. WINGATE, W.S. HALL, H.O. WHITE, J.A. COTTON, W.B. PARKER, and R.B. MCNUTT. 1961. Soil Survey of Calhoun County. USDA Soil Conservation Service, Washington, D.C.

HARPER, R.M. 1905. Some noteworthy stations for *Pinus palustris.* Torreya 5:55–60.

HARPER, R.M. 1913. Economic botany of Alabama. Monograph 8. Part 1. Alabama Geological Survey, Tuscaloosa, Alabama.

HARPER, R.M. 1928. Economic botany of Alabama. Monograph 9. Part 2. Alabama Geological Survey, Tuscaloosa, Alabama.

HARPER, R.M. 1943. Forests of Alabama. Monograph 10. Geological Survey of Alabama, Tuscaloosa, Alabama.

KUSH, J.S., R.K. BOLTON, T.R. BOTTENFIELD, R.S. MELDAHL, and R.M. FARRAR. 1989. Longleaf pine crown relationships: a preliminary analysis. p. 433–436. *In:* Miller, J.H. (ed.). Proceedings of the 5th Biennial Southern Silvicultural Research Conference. Gen. Tech. Rep. SE-42. USDA Forest Service, Southern Forest Experiment Station, Asheville, North Carolina.

LINDENMAYER, D.B. and J.F. FRANKLIN. 1997. Managing stand structure as part of ecologically sustainable forest management in Australian mountain-ash forests. Conserv. Biol. 11:1053–1068.

LIPPS, E.L. 1966. Plant communities of a portion of Floyd County, Georgia—especially the Marshall Forest. Ph.D. dissertation, University of Tennessee, Knoxville, Tennessee.

LORIMER, C.G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. Ecology 61:1169–1184.

MEANS, D.B. 1996. The longleaf ecosystem, going, going ... p. 210–219. *In:* Davis, M.B. (ed.). Eastern old-growth forests: prospects for rediscovery and recovery. Island Press, Washington, D.C.

MELDAHL, R.S., N. PEDERSON, J.S. KUSH, and J.M. VARNER. 1999. Dendrochronological investigations of climate and competitive effects on longleaf pine growth. p. 265–285. *In:* Wimmer, R. and R.E. Vetter (eds.). Tree ring analysis: biological, methodological, and environmental aspects. CAB International, Wallingford, United Kingdom.

MOHR, C.T. 1897. The timber pines of the southern United States. USDA Division of Forestry Bull. 13, Washington, D.C.

NEEL, L. 1971. Some observations and comments on the red-cockaded woodpecker in the Thomasville-Tallahassee Game Preserve Region. p. 137–139. *In:* Thompson, R.L. (ed.). The ecology and management of the red-cockaded woodpecker. USDI Bureau of Sport Fisheries and Wildlife and Tall Timbers Research Station,Tallahassee, Florida.

NOEL, J.M., W.J. PLATT, and E.B. MOSER. 1998. Structural characteristics of old- and second-growth stands of longleaf pine (*Pinus palustris*) in the Gulf Coastal Region of the U.S.A. Conserv. Biol. 12:533–548.

NOSS, R.F., E.T. LAROE, and J.M. SCOTT. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. USDI National Biological Service, Biol. Rep. 28, Washington, D.C.

OLIVER, C.D. and B.C. LARSON. 1990. Forest Stand Dynamics. McGraw-Hill, New York, New York.

OUTCALT, K.W. 2000. Occurrence of fire in longleaf pine stands in the southeast United States. p. 178–182. *In:* Moser, W.K. and C.F. Moser (eds.). Proceedings of the 21st Tall Timbers Fire Ecology Conference. Tall Timbers Research Station, Tallahassee, Florida.

OUTCALT, K.W. and R.M. SHEFFIELD. 1996. The longleaf pine forest: trends and current conditions. Resource Bulletin SRS-9. USDA Forest Service, Southern Research Station, Asheville, North Carolina.

PALIK, B.J. and N. PEDERSON. 1996. Overstory mortality and canopy disturbances in longleaf pine ecosystems. Can. J. For. Res. 26:2035–2047.

PALIK, B.J., R.J. MITCHELL, G.A. HOUSEAL, and N. PEDERSON. 1997. Effects of canopy structure on resource availability and seedling response in a longleaf pine ecosystem. Can. J. For. Res. 27:1458–1464.

PESSIN, L.J. 1934. Annual ring formation in *Pinus palustris* seedlings. Amer. J. Bot. 21:599–603.

PLATT, W.J. and S.L. RATHBUN. 1993. Population dynamics of an old-growth population of longleaf pine (*Pinus palustris*). p. 200–214. *In:* Herman, S.H. (ed.). Proceedings of the 18th Tall Timbers Fire Ecology Conference. Tall Timbers Research Station, Tallahassee, Florida.

PLATT, W.J., G.W. EVANS, and S.L. RATHBUN. 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). Amer. Naturalist 131:491–525.

REED, F.W. 1905. A working plan for forest lands in central Alabama. USDA Forest Service, Bull. 68, Washington, D.C.

REED, M.B., C.E. CANTLEY, and J.W. JOSEPH. 1994. Fort McClellan: a popular history. New South Associates, Stone Mountain, Georgia.

RHOADES, R.W. 1999. Ice storm damage in a small valley in southwestern Virginia. Castanea 64:243–251.

SARGENT, C.S. 1884. Report on the forests of North America (exclusive of Mexico). 10th US Census Report. Volume 9. Washington, D.C.

SAS INSTITUTE. 1990. SAS/STAT User's Guide Version 6. Volume 2. SAS Institute Inc., Cary, North Carolina.

SCHWARZ, G.F. 1907. The longleaf pine in virgin forest: a silvical study. Wiley, New York, New York.

VARNER, J.M. 2000. Species composition, structure, and dynamics of old-growth mountain longleaf pine forests of Fort McClellan, Alabama. M.S. thesis, Auburn University, Auburn, Alabama.

VARNER, J.M. and J.S. KUSH. 2001. Old-growth longleaf pine forests—filling in the blanks. p. 204–208. *In:* Kush, J.S. (ed.). Proceedings of the 3rd Longleaf Alliance Conference. The Longleaf Alliance, Auburn, Alabama.

VARNER, J.M., J.S. KUSH, and R.S. MELDAHL. 2003. Vegetation of frequently burned old-growth longleaf pine (*Pinus palustris* Mill.) savannas on Choccolocco Mountain, Alabama, USA. Nat. Areas J. 23:43–52.

WAHLENBERG, W.G. 1946. Longleaf pine: its use, ecology, regeneration, protection, and management. Charles Lathrop Pack Forestry Foundation and USDA Forest Service, Washington, D.C.

WARE, S., C.C. FROST, and P.D. DOERR. 1993. Southern mixed hardwood forest: the former longleaf pine forest. p. 447–493. *In:* Martin, W.H., S.G. Boyce, and A.C. Echternacht (eds.). Biodiversity of the southeastern United States: upland terrestrial communities. Wiley, New York, New York.

Received July 24, 2002; Accepted December 16, 2002.