RESEARCH ARTICLE

# Vegetation of Frequently Burned Old-Growth Longleaf Pine (*Pinus palustris* Mill.) Savannas on Choccolocco Mountain, Alabama, USA

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**ABSTRACT:** Fire-maintained longleaf pine (*Pinus palustris* Mill.) savannas are imperiled throughout their range in the United States, reduced in extent by 97% since European settlement. Only half of extant stands show evidence of fire; fire suppression has led to dramatic changes in composition and declines in plant diversity. Examples of pristine vegetation are known for most of longleaf pine's distinct regions—a notable exception being mountainous communities in Alabama and Georgia, USA, collectively termed the mountain longleaf pine savannas. We sampled over- and understory vegetation in two frequently burned old-growth mountain longleaf pine stands at Fort McClellan, a U.S. Army garrison in the Blue Ridge Physiographic Province of Alabama. Over the spring, summer, and fall 1999 study period, 82 native plant species were encountered in plots, representing 60 genera and 35 families. Overstory composition was dominated by longleaf pine, with blackjack oak (*Quercus marilandica* Muenchh.) and sand hickory (*Carya pallida* [Ashe] Engl. & Graeb.) as co-dominants in both stands. Understory communities were species-rich, dominated by grasses (principally *Andropogon ternarius* Michx.), asters (*Coreopsis major* Walt., *Chrysopsis graminifolia* [Michx.] Elliott, *Helianthus microcephallus* Torrey & Gray, *Solidago odora* Ait., and others), and many legumes. Non-native species were not encountered in sampling plots. Evidence suggests that historic fires in mountain longleaf pine savannas were frequent (1-to 5-y return interval) and frequent fire is needed to maintain this ecosystem in the contemporary southeastern landscape.

### Vegetación en Savanas Maduras de Pino de Hoja Larga (*Pinus palustris* Mill.) Frecuentemente Quemadas en Choccolocco Mountain, Alabama, USA

**RESUMEN:** Las savanas de pino de hoja larga (*Pinus palustris* Mill.) mantenidas con fuego están en peligro en toda su distribución en Estados Unidos, y fueron reducidas en el 97% de su extensión desde el asentamiento de los europeos. Solamente la mitad de los lotes muestran evidencia de fuego; la supresión del fuego ha llevado a cambios dramáticos en la composición y la disminución en la diversidad de plantas. Se conocen ejemplos de vegetación prístina para la mayoría de las distintas regiones de pino de hoja larga – una notable excepción son la comunidades montañosas en Alabama y Georgia, USA, colectivamente denominadas las savanas montañosas de pino de hoja larga. Muestreamos la vegetación del dosel y del soto bosque en dos lotes frecuentemente quemados de pino de hoja larga maduros en Fort McClellan, una guarnición del ejercito en la provincia fisiográfica de Blue Ridge en Alabama. Durante el período de estudio de primavera, verano y otoño de 1999, 82 plantas nativas fueron encontradas en los lotes, representando 60 géneros y 35 familias. La composición del dosel estuvo dominada por el pino de hoja larga, con el roble blackjack (*Quercus marilandica* Muenchh.) y el nogal arena (*Carya pallida* [Ashe] Engl. & Graeb.) como codominantes en ambos lotes. Las comunidades del sotobosque fueron ricas en especies, dominadas por pastos (principalmente *Andropogon ternarius* Michx.), ásters (*Coreopsis major* Walt., *Chrysopsis graminifolia* [Michx.] Elliott, *Helianthus microcephallus* Torrey & Gray, *Solidago odora* Ait., y otras), y muchas leguminosas. No encontramos especies exóticas en los lotes de muestreo. La evidencia sugiere que los fuegos históricos en las savanas montañosas de pino de hoja larga fueron frecuentes (intervalos 1 a 5 años) y el fuego frecuente es necesario para mantener este ecosistema en el paisaje contemporáneo del sudeste.

*Index terms:* fire regimes, mountain longleaf pine savanna, *Pinus palustris*, presettlement conditions, species composition

## INTRODUCTION

Savannas and forests dominated by longleaf pine (*Pinus palustris* P. Miller) and a diverse bunchgrass-dominated herbaceous layer covered an estimated 37 million ha of the southeastern United States prior to European settlement (Frost 1993). Their open structure and diverse plant species assemblages (Peet and Allard 1993) were maintained by frequent (once every 1 to 10 y), low-intensity surface fires that were ignited by lightning and, in the recent past, Native Americans (Bartram 1791, Komarek 1964, Robbins and Myers 1992). Longleaf pine savannas dominated portions of the Coastal Plain, Piedmont, Cumberland Plateau, Ridge and Valley, and Blue Ridge physiographic provinces from coastal Virginia through eastern Texas (Figure 1). Because fires in longleaf pine savannas often carry into adjacent communities (e.g., pitcher plant [*Sarracenia* L. spp.] bogs, shrub bogs, cypress strands), these savannas have been referred to as the keystone community of the southeastern landscape (Noss 1989, Myers 1990, Means 1996).

Since European settlement, land conversion has resulted in a reduction of longleaf pine acreage to less than 3% of its former range, covering fewer than 1.2 million ha (Outcalt and Sheffield 1996). The remaining acreage contains few pristine stands or landscapes (Ware et al. 1993, Means 1996); indeed only about half of the remnants show evidence of fire (Outcalt 2000). With the precipitous decline of longleaf pine, the associated flora and fauna have also suffered. A recent evaluation lists longleaf pine savannas and forests as the second most endangered ecosystems in the United States, second only to the Florida Everglades (Noss et al. 1995).

Mountain longleaf pine savannas are a loosely defined community type in northern Alabama and Georgia. No rigorous delineation of a "mountain" (often termed "montane") type exists, though most observers agree that Blue Ridge, Ridge and Valley, and Cumberland Plateau sites are within the mountain region. If the Piedmont Physiographic Province is included (Figure 1), less than 40,000 ha of mountain longleaf pine ecosystems remained by 1995 (Outcalt and Sheffield 1996, Varner 2000). Of this total, only 20 ha were identified as old growth (Varner 2000).

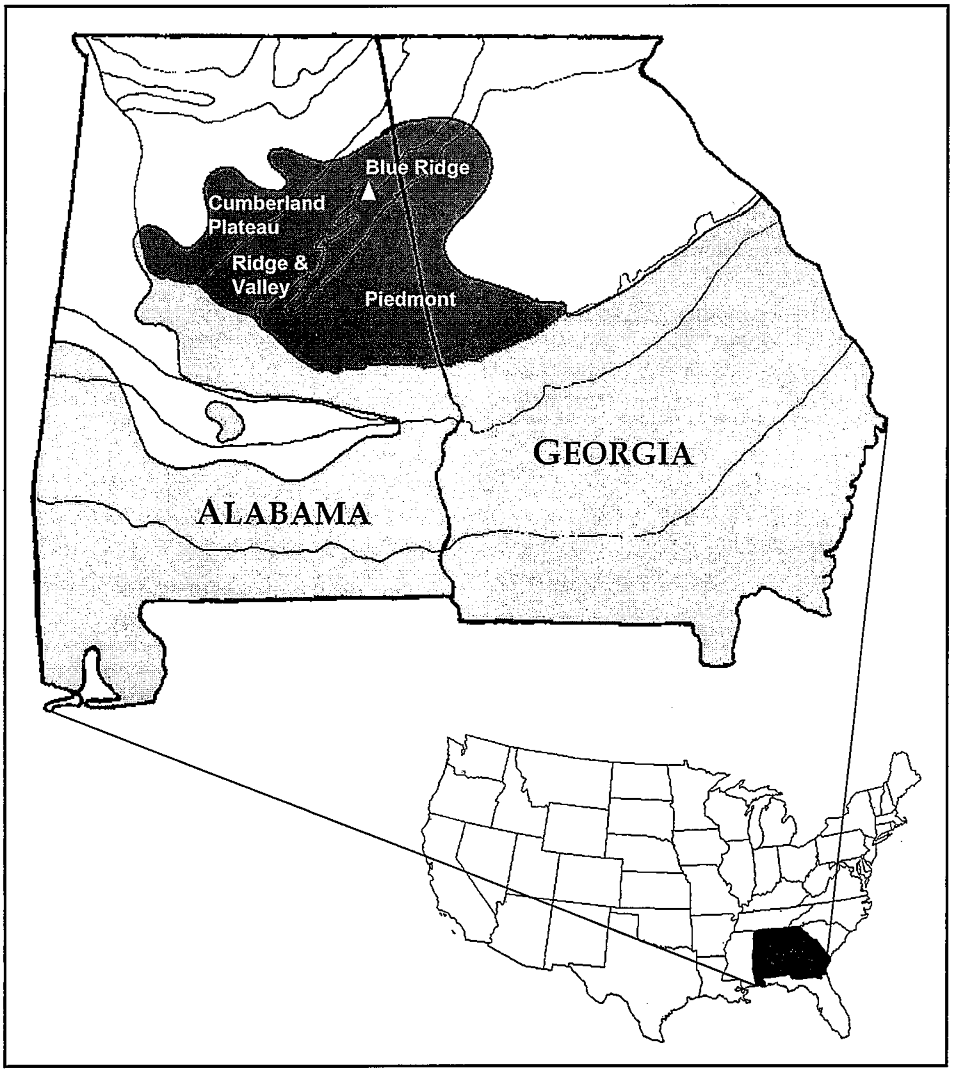


**Figure 1. Native range of longleaf pine in Alabama and Georgia, USA (light and dark shaded areas). Dark shaded region denotes the range of mountain longleaf pine savannas and forests. Physiographic provinces represented by this region are in white type. The white triangle represents the approximate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

Fire is noticeably absent or much reduced over most of the southeastern mountain landscape. In the absence of frequent, low-intensity (every 1 to 5 y) fires, Coastal Plain longleaf pine savannas succeed to a closed-canopy, mixed hardwood forest, termed the Southern Mixed Hardwood Forest (SMHF) (Ware et al. 1993). In the mountain region, the same successional trajectory prevails, with communities shifting toward either the SMHF (Ware et al. 1993) or Oak-Hickory-Pine (OHP) forest (Kuchler 1964, Skeen et al. 1993). Typical successional overstory species in the mountains include red maple (*Acer rubrum* L.), several oaks (particularly *Quercus velutina* Lam. and *Q. prinus* L.), other pines (*Pinus taeda* L., *P. echinata* Mill., and *P. virginiana* Mill.), sourwood (*Oxydendrum arboreum* [L.] DC), and blackgum (*Nyssa sylvatica* Marsh.) (Golden 1979, Maceina 1997, Varner 2000). Understory successional species include many shrubs, greenbrier (*Smilax rotundifolia* L.), and lowbush blueberry (*Vaccinium pallidum* Chapman), the latter often forming dense, monospecific stands in infrequently burned stands (Golden 1979, Varner 2000). Land use and contemporary forest management in the mountain longleaf pine region have created isolated patches of erratically burned vegetation within a larger fire-suppressed forested mosaic (Alabama Natural Heritage Program 1994, Varner 2000), making approximations of pristine or presettlement conditions difficult.

Although mountain pinelands represent one of the most unique longleaf pine ecosystems—they occur at high elevations (up to 600 m above msl), commonly experience ice and snow storms, are located at the maximal distance from tropical storms, occupy extremely dissected topography, and are in the most climatically distinct region of longleaf pine's natural range (Craul 1965)—they have undergone very little study. Surveys of longleaf pine vegetation have been undertaken in the western Gulf Coastal Plain (Marks and Harcombe 1981, Schafale and Harcombe 1983, Bridges and Orzell 1989, Harcombe et al. 1993), eastern Gulf Coastal Plain (Penfound and Watkins 1937, Clewell 1986, Peet and Allard 1993, Drew et al. 1998), Atlantic Coastal Plain and Sandhills (Harper 1906, Walker and Peet 1983, Frost and Musselman 1987, Gilliam et al. 1993, Peet and Allard 1993), Upper Coastal Plain (Beckett and Golden 1982), and Piedmont (Golden 1979). In contrast, mountain longleaf pine ecosystems in the Ridge and Valley, Blue Ridge, and Cumberland Plateau have undergone very little study (but see Maceina et al. 2000).

Previous research on longleaf pine communities in the mountain region have been based on degraded stands and were generally limited in scope. Golden (1979) analyzed longleaf pine communities in the lower Piedmont Province, providing quantitative data, albeit based on stands with infrequent fire and dubious management histories. Using research based at Fort McClellan, Alabama, USA, Maceina (1997) described the overstory species composition and successional trajectory of a second-growth mountain longleaf pine stand. Maceina's tract had an erratic burning history and was subject to mechanical scraping several years prior to her survey (Maceina 1997). In the same tract, Maceina et al. (2000) surveyed the mountain longleaf pine flora utilizing meander surveys, a method that does not easily allow for comparisons or quantification. Similarly, Whetstone and others (1996) observed 871 plant species in their survey of Fort McClellan's landscape. However, they did not attribute species to specific community types, nor did they recognize mountain longleaf pine communities in their survey. From these reports emerge an incomplete description of the vegetation and a rudimentary understanding of mountain longleaf pine community composition, confounded by a lack of data or understanding from pristine sites.

We initiated a study in 1998 to address the lack of data and understanding of mountain longleaf pine communities. The primary objective of this study was to survey and quantify overstory and understory plant species composition of two frequently burned old-growth longleaf pine communities. These benchmark data and their information could then be utilized for identification, conservation, and restoration of this rare ecosystem. An additional objective was to establish permanent plots for long-term studies on this disappearing community type.

## METHODS

### Study Areas

Fort McClellan is a 7,300-ha U.S. Department of Defense Army garrison in eastern Calhoun County, northeastern Alabama (33°42′ N, 85° 45′ W). Fort McClellan contains a large portion of Choccolocco Mountain and its spur ridges, all capped with Weisner quartzite. Climate is warm and humid, with a mean annual temperature of 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 125 cm, with small amounts falling as ice and snow (Harlin et al. 1961, Craul 1965).

At Fort McClellan, we selected two stands with histories of frequent burning (1- to 3-y cycles) and an old-growth longleaf pine overstory (oldest age classes preceding European settlement, ca. 1850). The two stands, hereafter Caffey Hill and Red-tail Ridge, were located at ca. 450 and 350 m above msl, respectively. Caffey Hill is an upper slope stand covering 1.5 ha abutting a downslope 250-ha matrix of younger, frequently burned stands. Red-tail Ridge spans a mid- to upper slope position covering 1.8 ha abutting a frequently burned, somewhat disturbed 20-ha tract below on side slopes. At both sites, soils were mapped as Rough Stony Land–Sandstone, a miscellaneous Typic Udult with many outcrops of quartzite and sandstone bedrock and loose rock fragments, representative of many mountain longleaf pine ecosystems (Craul 1965). These sites are located upslope of, and often intergrade with, the Anniston soil series. Anniston soils are clayey, kaolinitic, thermic Rhodic Paleudults. Surface soils are loams, transitioning to clay-loams in subsoils (Harlin et al. 1961). Slopes averaged 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.

### Data Collection

#### *Understory Species Composition*

Within each intensive study area, we installed plot centers and vegetation sampling quadrats (Caffey Hill—five plots; Red-tail Ridge—four plots). From each plot center, four 1.1-m × 1.1-m quadrats were placed in cardinal directions, each 5 m from plot center, for a total of 20 quadrats at Caffey Hill and 16 at Red-tail Ridge. We sampled all quadrats once during spring (April), summer (June), and fall (September) 1999. Within each quadrat, all plant species were identified (nomenclature according to Kartesz 1994) and assigned an approximate cover value (1% to 100%) based on visual estimation. Since sampling took place over three seasons, all three (spring, summer, and fall) cover values were averaged for calculations. Relative frequency (RF) and relative cover (RC) were calculated for both sites. Importance values (IV) were calculated for individual species as the sum of relative frequency (RF) and relative cover (RC), for a potential importance value equal to 200.

To describe and compare these communities, we assigned each species a form class. Tree seedlings (T) were classified as woody species capable of reaching the canopy. Shrubs (S) were classified as woody species normally incapable of reaching the canopy. The other two classes were forbs, including woody vines (F), and grasses (G).

#### *Overstory Species Composition*

All longleaf pine stems (100% sample at each site) > 2.5 cm dbh (where dbh = diameter at breast height [1.37 m]) within the two intensive study areas were mapped (azimuth and horizontal distance to plot centers) and measured. All other overstory species > 2.5 cm dbh were identified, counted, and measured (dbh only). From these measurements, average and relative stem density (trees ha$^{-1}$; RD) and average and relative basal area (m$^2$ ha$^{-1}$; RBA) were calculated. Importance values were calculated as the sum of RD and RBA, for a potential importance value of 200.

Long-term fire histories of the two stands are, as with all but a handful of sites in the Southeast, unavailable beyond the recent forest management era (1960 to present). Assessment of longer term fire history can be approximated based on overstory species composition. While understory communities are unlikely to contain species that are relicts of fire suppression, overstory species have a much higher probability of remaining, even after long-term resumption of active fire management (Boyer 1990b). To detect relicts and overstory species stability, we used under-representation techniques (Golden 1979). Under-representation, as defined by Golden (1979), is the condition where there are fewer individuals in two consecutive size classes than in the subsequent larger size class. This technique identifies species that colonized at a point in time, but at present are failing to regenerate; that is they are relicts of past favorable ecological conditions. Species that either (1) were under-represented at both sites, or 2) were under-represented at one site and absent at the other, were classified as relict species.

## RESULTS

### Understory Species Composition

Seventy-two understory plant species were encountered over the three sampling periods. Though most species were represented at both sites (42), Red-tail Ridge had more species and higher cover values than Caffey Hill (Table 1). Red-tail Ridge had more forb (47 versus 34) and legume (10 versus 7) species than Caffey Hill. Numbers of grass (Poaceae), aster (Asteraceae), shrub, and tree species were similar between sites. Both sites were characterized by a diverse groundcover layer, dominated by *Andropogon ternarius* Michx., *Chrysopsis graminifolia* (Michx.) Elliott, *Coreopsis major* Walt., *Euphorbia corollata* L., *Helianthus microcephalus* Torrey & Gray, *Panicum commutatum* Schult.,

**Table 1. Understory plant species (stems < 2.5 cm dbh) list from two frequently burned old-growth mountain longleaf pine stands located at Fort McClellan, Alabama, USA. Values listed are Importance Values, where IV = Relative Frequency + Relative Cover. Asterisks in columns denote IVs < 1. Both frequency and cover values were averaged over the three seasonal samples for each quadrat. Form refers to plant form, either tree (T), shrub (S), forb (F), or grass (G). Nomenclature follows Kartesz 1994.**

| FAMILY | | Importance Values | |
|---|---|---|---|
| *Species* | Form | Caffey Hill | Red-tail Ridge |
| AMARYLLIDACEAE | | | |
| *Hypoxis hirsuta* (L.) Coville | F | 1 | 1 |
| ANACARDIACEAE | | | |
| *Rhus copallina* L. | S | 12 | 9 |
| *Rhus radicans* L. | F | * | 0 |
| *Rhus toxicodendron* L. | F | 3 | 0 |
| ANNONACEAE | | | |
| *Asimina parviflora* (Michx.) Dunal | S | 3 | * |
| APIACEAE | | | |
| *Angelica venenosa* (Greenway) Fernald | F | 0 | 1 |
| ASCLEPIADACEAE | | | |
| *Asclepias amplexicaulis* Smith | F | 0 | 1 |
| ASTERACEAE | | | |
| *Aster dumosus* L. | F | 1 | 0 |
| *Aster patens* Aiton | F | 2 | 8 |
| *Aster undulatus* L. | F | 2 | 6 |
| *Chrysopsis graminifolia* (Michx.) Elliott | F | 9 | 6 |
| *Coreopsis major* Walter | F | 13 | 3 |
| *Elephantopus tomentosus* L. | F | 2 | 0 |
| *Helianthus microcephalus* Torrey & Gray | F | 6 | 13 |
| *Helianthus mollis* Lamarck | F | 1 | * |
| *Krigia biflora* (Walter) Blake | F | 2 | * |
| *Liatris graminifolia* Willdenow | F | 1 | 1 |
| *Silphium terebenthinaceum* Jacquin | F | 0 | 3 |
| *Solidago erecta* Pursh | F | 5 | * |
| *Solidago odora* Aiton | F | 10 | 4 |
| CAMPANULACEAE | | | |
| *Specularia perfoliata* L. A.DC | F | 1 | 1 |
| COMMELINACEAE | | | |
| *Tradescantia hirsuticaulis* Small | F | 0 | * |
| CONVULVULACEAE | | | |
| *Ipomoea lacunosa* L. | F | 0 | 3 |

*continued*

*Pteridium aquilinum* L., *Rhus copallina* L., and *Solidago odora* Ait. Asters, grasses, and legumes were the best represented families, together comprising 50% and 56% importance at Caffey Hill and Red-tail Ridge, respectively. Herbaceous species, in general, were most important at both sites, accounting for 71.5% of total understory importance at Caffey Hill, and 85% at Red-tail Ridge. Seedlings of tree species were rare, together comprising only 5% and 4% of total importance at Caffey Hill and Red-tail Ridge. Shrubs were also rare, accounting for 23.5% and 11% total importance at Caffey Hill and Red-tail Ridge. Non-native species were not encountered in any of the 36 sampling quadrats in any season, or at either of the two sites outside of sampling quadrats.

Individual sample species richness maxima were 22 species per quadrat at Red-tail Ridge and 19 per quadrat at Caffey Hill. The lowest individual samples at each site were 8 and 10 species per quadrat. Cover values per quadrat averaged 82% (± 6.4%) at Red-tail Ridge, 68% (± 5.3%) at Caffey Hill. Individual quadrat cover maxima / minima were 109% / 50% at Red-tail Ridge, and 83%/ 45% at Caffey Hill.

## Overstory Species Composition

Eighteen overstory (dbh >2.5 cm) woody plant species were recorded at the two study sites; Red-tail Ridge had 16 species, Caffey Hill 9 species (Table 2). Longleaf pine was the most frequent and important species at both sites, representing 63.3% and 94.5% of basal area at Red-tail Ridge and Caffey Hill, respectively. Total basal area at Red-tail Ridge and Caffey Hill were 20.6 $m^2$ $ha^{-1}$ and 8.8 $m^2$ $ha^{-1}$, respectively. Overstory density at Red-tail ridge and Caffey Hill was 721 and 535 trees $ha^{-1}$, with longleaf pine representing 39.2% and 55.6% of all trees at each site. The most important species at both sites were longleaf pine, blackjack oak, sand hickory, and to a lesser extent, blackgum and rock chestnut oak (*Quercus prinus* L.).

Only three of the eighteen species were (1) present at both sites, and (2) not significantly underrepresented (<25% of size classes underrepresented): longleaf pine,

**Table 1,** ***continued***

| **FAMILY** | | **Importance Values** | |
|---|---|---|---|
| ***Species*** | **Form** | **Caffey Hill** | **Red-tail Ridge** |
| EBENACEAE | | | |
| *Diospyros virginiana* L. | S | 8 | 3 |
| ERICACEAE | | | |
| *Vaccinium arboreum* Marshall | S | 4 | 6 |
| EUPHORBIACEAE | | | |
| *Euphorbia corollata* L. | F | 9 | 9 |
| FABACEAE | | | |
| *Clitoria mariana* L. | F | 3 | 6 |
| *Desmodium viridiflorum* (L.) De Candolle | F | 0 | 1 |
| *Galactia volubilis* (L.) Britton | F | 1 | 4 |
| *Lespedeza intermedia* (Watson) Britton | F | 1 | 2 |
| *Lespedeza procumbens* Michx. | F | 1 | * |
| *Lespedeza stuevei* Nutt. | F | 0 | 1 |
| *Lespedeza virginica* (L.) Britton | F | 0 | 3 |
| *Rhynchosia tomentosa* (L.) Hook. & Arn. | F | 5 | 5 |
| *Senna marilandica* (L.) Link | F | 2 | 2 |
| *Tephrosia virginiana* (L.) Pers. | F | 5 | 6 |
| FAGACEAE | | | |
| *Quercus marilandica* Muenchh. | T | 6 | 3 |
| *Quercus prinus* L. | T | 0 | * |
| HYPERICACEAE | | | |
| *Hypericum gentianoides* (L.) B. S. P. | F | 1 | * |
| *Hypericum hypericoides* (L.) Crantz. | F | 0 | * |
| *Hypericum punctatum* Bush | F | * | * |
| IRIDACEAE | | | |
| *Iris verna* L. | F | 0 | 3 |
| *Sisyrinchium angustifolium* Mill. | F | * | 1 |
| JUGLANDACEAE | | | |
| *Carya pallida* (Ashe) Engler & Graebner | T | 8 | 5 |
| LAMIACEAE | | | |
| *Salvia urticifolia* (L.) | F | 2 | 3 |
| LAURACEAE | | | |
| *Sassafras albidum* (Nutt.) Nees. | S | 20 | 0 |
| NYSSACEAE | | | |
| *Nyssa sylvatica* Marshall | T | 0 | 1 |

*continued*

blackjack oak, and sand hickory (Table 3). In addition to the previous three species, blackgum, post oak (*Q. stellata* Wagenh.), sassafras (*Sassafras albidum* (Nutt.) Nees.), tree sparkleberry (*Vaccinium arboreum* Marsh.), red maple, sourwood, flowering dogwood (*Cornus florida* L.), and sweetgum (*Liquidambar styraciflua* L.) were well represented in our two stands. Relict species included rock chestnut oak, shortleaf pine (*Pinus echinata* Mill.), black cherry (*Prunus serotina* Ehrh.), black oak (*Q. velutina*), Virginia pine, Sonderegger pine (*P.* X *sondereggeri* H. H. Chapm.), and loblolly pine.

## DISCUSSION

### Understory Species Composition

Fire-maintained understory communities in longleaf pine savannas are renowned for being extremely species-rich (Walker and Peet 1983, Peet and Allard 1993). These two stands at Fort McClellan were no exception. First, even with limited sampling, 72 native understory plant species were encountered. Single sample maxima of 22 and 19 species per 1.21 $m^2$ quadrat are comparable to those found at many sites listed in Peet and Allard (1993). Our findings are significant, in light of the fact that data from mountain longleaf pine communities were not included in Peet and Allard (1993) or any other works.

Very few tree seedlings and saplings were found in sampling the two study stands. Longleaf pine, which overwhelmingly dominated the overstory of both sites (Table 2), was only encountered as a seedling once at Caffey Hill, and none were observed at Red-tail Ridge. As with the longleaf pine overstory, seedlings and saplings are concentrated in even-aged patches under gaps in the canopy (Wahlenberg 1946, Brockway and Outcalt 1998). Therefore, although seedling stocking at Caffey Hill was excellent in areas (pers. observation, J.M. Varner), our sampling revealed very few seedlings. At Red-tail Ridge, due to its proximity to several military firing ranges, nearly annual burning had taken place for 11 y prior to sampling, so seedlings were unable to grow to a size (ca. 0.8 cm ground-line diameter) where they could

**Table 1, *continued***

| FAMILY | | Importance Values | |
|---|---|---|---|
| *Species* | Form | Caffey Hill | Red-tail Ridge |
| ONAGRACEAE | | | |
| *Circaea lutetiana* Aschers. & Magnus | F | 0 | 1 |
| *Gaura longiflora* Spach | F | 2 | 1 |
| OXALIDACEAE | | | |
| *Oxalis dillenii* Jacquin | F | 1 | 4 |
| *Oxalis violacea* L. | F | 0 | 1 |
| PINACEAE | | | |
| *Pinus echinata* Mill. | T | 0 | 1 |
| *Pinus palustris* Mill. | T | 1 | 0 |
| POACEAE | | | |
| *Andropogon ternarius* Michx. | G | 16 | 20 |
| *Panicum commutatum* Schult. | G | 9 | 5 |
| *Panicum virgatum* L. | G | * | 3 |
| *Panicum* spp. | G | 3 | 0 |
| *Poa* spp. | G | 0 | * |
| *Piptochaetium avenacea* L. | G | * | 8 |
| POLEMONIACEAE | | | |
| *Phlox amoena* Sims | F | 0 | 1 |
| POLYPODIACEAE | | | |
| *Asplenium platyneuron* (L.) Oakes | F | 0 | 1 |
| *Pteridium aquilinum* L. | F | 10 | 9 |
| RUBIACEAE | | | |
| *Galium pilosum* Ait. | F | 0 | 4 |
| SAXIFRAGACEAE | | | |
| *Hydrangea quercifolia* Bartram | S | 0 | 4 |
| SCROPHULARIACEAE | | | |
| *Agalinus purpurea* (L.) Pennell | F | 0 | 1 |
| *Aureolaria pedicularia* (L.) Raf. | F | 4 | 0 |
| *Pentstemon pallidus* Small | F | 0 | 2 |
| *Seymeria cassioides* (Walt.) Blake | F | * | 0 |
| SMILACACEAE | | | |
| *Smilax glauca* Walt. | F | 4 | 5 |
| VIOLACEAE | | | |
| *Viola palmata* L. | F | 0 | 2 |
| *Viola pedata* L. | F | 0 | 1 |

Table 2. Overstory (stems > 2.5 cm dbh) species of two frequently burned (1–3 year return interval) old-growth mountain longleaf pine stands at Fort McClellan, Alabama, USA. Importance values are sums of relative density (trees $ha^{-1}$) and relative basal area ($m^2 ha^{-1}$), for a potential sum of 200. BA=basal area, IV=importance value.

| | Caffey Hill | | | Red-tail Ridge | | |
|---|---|---|---|---|---|---|
| Species (18) | Trees $ha^{-1}$ | BA ($m^2ha^{-1}$) | IV | Trees $ha^{-1}$ | BA ($m^2ha^{-1}$) | IV |
| *P. palustris* | 282.82 | 13.01 | 102.5 | 297.64 | 8.29 | 150.2 |
| *Q. marilandica* | 163.23 | 1.44 | 29.6 | 174.35 | 0.32 | 36.2 |
| *Carya pallida* | 110.09 | 2.30 | 26.4 | 20.34 | 0.04 | 4.3 |
| *Nyssa sylvatica* | 64.96 | 0.95 | 13.6 | 4.36 | 0.02 | 1.0 |
| *Q. prinus* | 20.94 | 0.98 | 7.7 | 21.07 | 0.07 | 4.7 |
| *P. echinata* | 13.41 | 0.57 | 4.6 | | | |
| *Quercus stellata* | 18.79 | 0.34 | 4.3 | 1.45 | <0.01 | 0.3 |
| *Prunus serotina* | 17.18 | 0.32 | 3.9 | | | |
| *Quercus velutina* | 6.44 | 0.25 | 2.1 | 5.09 | 0.01 | 1.1 |
| *Sassafras albidum* | 9.45 | 0.01 | 1.9 | | | |
| *P. virginiana* | 3.75 | 0.23 | 1.6 | | | |
| *Vaccinium arboreum* | 8.59 | 0.03 | 1.3 | | | |
| *Acer rubrum* | 4.83 | 0.06 | 1.0 | | | |
| *Oxydendrum arboreum* | 2.68 | 0.04 | 0.6 | 1.45 | 0.01 | 0.4 |
| *Cornus florida* | 2.15 | 0.01 | 0.3 | | | |
| *P. X sondereggeri* | 0.54 | 0.02 | 0.2 | | | |
| *P. taeda* | 0.54 | 0.01 | 0.1 | | | |
| *Liquidambar styraciflua* | 0.54 | <0.01 | 0.1 | | | |
| Totals | 721.48 | 20.56 | | 535.20 | 8.76 | |

survive even cool surface fires (Boyer 1990a). Longleaf pine saplings (< 10 cm dbh) were abundant at Caffey Hill, and less common at Red-tail Ridge (Varner 2000), again the latter due to the aggressive military burning regimes. Other tree species seedlings were also rare (Table 1), resulting in under-representation of these normally fire-tolerant species (Table 3).

Shrub and small tree species were rare at both sites, except for sassafras, winged sumac (*Rhus copallina* L.), and persimmon (*Diospyros virginiana* L.) (Table 1). Sassafras and persimmon, while both capable of reaching the canopy, are common as understory species in frequently burned longleaf pine savannas throughout the Southeast (Peet and Allard 1993). All three species are common longleaf pine associates, and are all somewhat fire-adapted. Furthermore, all three of these species were observed as small individuals, mostly less than 0.5 m tall (J.M. Varner, pers. observ.). Low shrub importance is a characteristic of frequently burned longleaf pine savannas throughout their range (Wahlenberg 1946, Boyer 1990a, Peet and Allard 1993, Landers and Boyer 1999).

Previous studies (Golden 1979, Maceina 1997) have described mountain longleaf pine ecosystems with similar composition, but often with obvious differences or signs of degradation. Golden (1979) found several common mountain associates (*Pteridium aquilinum, Tephrosia virginiana* [L.] Pers., *Vaccinium arboreum, Coreopsis major, Asimina parviflora* [Michx]. Dunal, and others) in longleaf pine stands in the Piedmont of Alabama. However, he also found several Coastal Plain species (*Symplocos tinctoria* [L.] L'Heritier, *Gelsemium sempervirens* [L.] Ait., and others) and co-dominance by southern red oak (*Q. falcata* Michx.), which typically is not found in mountain savannas. In fact, the composition reported by Golden was more similar to Upper Coastal Plain longleaf pine communities (Beckett and Golden 1982, Peet and Allard 1993). Finally, in contrast to other mountain longleaf pine community investigations (Golden 1979, Whetstone et al. 1996, Maceina et al. 2000), we found no non-native species in any of our 36 sampling quadrats. This finding suggests that prescribed fire is an effective management tool for maintenance of longleaf pine community integrity (Drew et al. 1998).

## Overstory Species Composition

Longleaf pine dominated both study sites, with importance values similar to those in other mountain longleaf pine communities (Golden 1979, Maceina 1997). Overstory co-dominants (blackjack oak and sand hickory) were typical of other sites in the Piedmont (Golden 1979), Upper Coastal Plain (Beckett and Golden 1982, Peet and Allard 1993), Fall Line Sandhills (Gilliam et al. 1993), and other Blue Ridge sites (Maceina 1997). Differences between these stands, while most pronounced in the herbaceous and shrub layers, can also be observed in tree species presence data. Co-dominants in the lower Piedmont (Golden 1979) and Upper Coastal Plain (Beckett and Golden 1982, Peet and Allard 1993) included southern red oak, flowering dogwood, post oak, loblolly pine, shortleaf pine, and sweetgum. Black oak and turkey oak (*Q. laevis* Walt.) were co-dominants in a fire-suppressed North Carolina Sandhills stand (Gilliam et al. 1993). Turkey oak, while known to occur in mountain longleaf pine stands at Fort McClellan (ANHP 1994, Varner 2000), is a rare mountain congener. Black oak is susceptible to high mortality where frequent fires occur, is a poor sprouter (Sander 1990), and therefore is an indicator of extended fire-free intervals. The aspect dominance—open canopy of longleaf pine with a patchy midstory of blackjack oak and sand hickory—common to both sites, and to frequently burned communities in the mountain region, is strikingly similar to Coastal Plain longleaf pine sites. As with Coastal Plain communities, deviations from this aspect suggest some history of fire exclusion or alteration.

**Table 3. Diameter class under-representation of overstory tree species in two frequently burned old-growth mountain longleaf pine stands at Fort McClellan, Alabama, USA. Bold type indicates relict species in our analysis. Nomenclature follows Kartesz (1994). * denotes the absence of that species at that particular site, or better conceptualized as total, or 100% under-representation.**

| | Percentage of Size Classes[a] with Under-representation[b] | |
|---|---|---|
| Species | Caffey Hill | Red-tail Ridge |
| *Pinus palustris* | 0 | 10 |
| *Quercus marilandica* | 0 | 0 |
| *Carya pallida* | 0 | 0 |
| *Nyssa sylvatica* | 50 | 0 |
| *Quercus prinus* | **17** | **17** |
| *Pinus echinata* | * | **25** |
| *Quercus stellata* | 0 | 29 |
| *Prunus serotina* | * | **17** |
| *Quercus velutina* | **20** | **40** |
| *Sassafras albidum* | * | 0 |
| *Pinus virginiana* | * | **44** |
| *Vaccinium arboreum* | * | 0 |
| *Acer rubrum* | * | 0 |
| *Oxydendrum arboreum* | 25 | 0 |
| *Cornus florida* | * | 0 |
| *Pinus* X *sondereggeri* | * | **50** |
| *Pinus taeda* | * | **33** |
| *Liquidambar styraciflua* | * | 0 |

[a] 5-cm size classes were used

[b] Under-representation, as defined in Golden (1979), is the condition where there are fewer individuals in two consecutive size classes than in the subsequent larger size class. Augmenting his definition with the condition that if a species is absent from a site, then it is also underrepresented. Therefore, if a species was underrepresented at one site and absent from the other, we classify it as a relict species. Percentage of size classes with under-representation was calculated as: % = # of size classes with consecutive under-representation / # of total size classes.

Co-dominant species were of limited importance in these mountain longleaf pine stands (most with IVs < 10 and/ or underrepresented; Tables 2 and 3). Maceina (1997), in a stand about 1 km from this Caffey Hill site, found similar trends in importance values for most of the same species, along with blackgum. At Red-tail Ridge and Caffey Hill, overstory importance was dominated by longleaf pine, blackjack oak, and sand hickory; all fire-adapted species. Longleaf pine's adaptations to fire are well known (e.g., Chapman 1932), and both blackjack oak and sand hickory are common associates of frequently burned longleaf pine savannas in Fall Line communities, and in the case of blackjack oak, throughout much of longleaf pine's range (Peet and Allard 1993). These three species were the only species well represented in all size classes (Table 3). Underrepresented species or atypical assemblages of establishing species indicate a new community trajectory, largely due to altered fire regimes (Golden 1979, Maceina 1997). Blackgum and others (most notably red maple, sweetgum, and sourwood) were not significantly underrepresented in the two study stands, but since they were absent or underrepresented at one site, the hypothesis can be made that with continued sampling of more stands, these species would be classified as relicts.

The higher than expected species richness (18 species) in the overstory was surprising for these frequently burned stands. Longleaf pine savannas are normally associated with remarkably low tree species diversity (Bartram 1791, Reed 1905, Schwarz 1907, Wahlenberg 1946, Boyer 1990a, Landers and Boyer 1999). Indeed, longleaf pine rarely co-occurs with other canopy trees (Landers and Boyer 1999). Its life history traits from seed to seedling to sapling to adult all require frequent fire, which few species can withstand (Wahlenberg 1946). Even though most species were of low importance (most with IV < 15; Table 2) or were under-represented (Table 3), their curious occurrence may be a product of a fire intensity mosaic or a relict of a past fire-free interval. Erratic fire behavior in these undulating, steep landscapes may aid in creation of patches of fire-intolerant species, as is the case with several oak species in Coastal Plain landscapes (e.g., *Quercus geminata* domes, Myers 1990). Similarly, an extended fire-free interval (a long enough period to allow for establishment and growth to a stage where fire-susceptibility was low, ca. 15 y or more) may have led to the establishment and survival of these normally fire-killed species. For the latter explanation, these atypical species will be killed by continued burning and lost without replacement in such a hostile seedling environment. Whether or not this fire-free interval was within some historical range of variability or was an extreme event cannot be stated with assurance. Further study should examine the spatial distribution of these fire-intolerant species, and their status should be monitored with continued burning applications.

Only a handful of longleaf pine communities in pristine condition can be found at Fort McClellan and elsewhere in the mountain region of Alabama and Georgia. Sampling of other frequently burned stands, particularly in these peripheral regions, will surely prove valuable and contribute to an approximation of presettlement landscape conditions in the southeastern United States. The next step that must be undertaken is preservation and management of remnant mountain longleaf pine community types. However, this step will only be possible when the role of fire as a dominant environmental and evolutionary force in mountain longleaf pine savannas is acknowledged.

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