

Vascular Flora of Longleaf Pine Woodlands after Wind Disturbance and Salvage Harvesting in the Alabama Fall Line Hills

Author(s): Jonathan S. Kleinman and Justin L. Hart

Source: Castanea, 83(2):183-195.

Published By: Southern Appalachian Botanical Society

https://doi.org/10.2179/17-148

URL: http://www.bioone.org/doi/full/10.2179/17-148

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms of use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

Vascular Flora of Longleaf Pine Woodlands after Wind Disturbance and Salvage Harvesting in the Alabama Fall Line Hills

Jonathan S. Kleinman¹* and Justin L. Hart¹

¹Department of Geography, University of Alabama, Tuscaloosa, Alabama 35487

ABSTRACT The Oakmulgee District of the Talladega National Forest is the largest remnant of the endangered longleaf pine (*Pinus palustris*) ecosystem in Alabama. A partial floristic survey using nested plots and survey plots was conducted May-July 2016 in longleaf pine woodlands of the Oakmulgee District that were differentially impacted by a 27 April 2011 EF3 tornado and a subsequent salvage harvesting operation. Vascular plants were identified and ranked by frequency of occurrence (rare, occasional, common, and abundant) in three disturbance categories: undisturbed, wind-disturbed, and compound-disturbed (wind-disturbed and salvage-harvested). Overall, 192 plant taxa in 68 families and 137 genera were documented. Plant taxonomic richness was lowest on undisturbed sites (90 taxa), greatest on wind-disturbed sites (160 taxa), and reduced on compounddisturbed sites (126 taxa). Although salvage harvesting reduced taxonomic richness, 46 of the 48 plant taxa unique to unharvested wind-disturbed sites were rare (occurred on <10% of nested plots). Moreover, undisturbed sites had only nine unique taxa, of which eight were rare. Decisions on whether to salvage harvest must consider the ecological significance of these rare plants. Wind- and compound-disturbed areas may recover toward predisturbance conditions, and the floristic list presented here provides the baseline to monitor this succession. The documented floristic composition also provides insight on short-term responses of vascular plants to differential disturbance impacts in an understudied region of the longleaf pine ecosystem.

Key words: Fall Line Hills, floristic composition, longleaf pine, *Pinus palustris*, salvage, wind.

INTRODUCTION The longleaf pine (*Pinus palustris* Mill.) ecosystem was once extensive in the southeastern United States, occupying ca. 37 million ha across the Coastal Plain, Piedmont, and Appalachian Highlands (Frost 2006). Regional decline of the longleaf pine ecosystem occurred in the late 1800s and early 1900s in association with turpentine production, agricultural land clearing, industrial-scale timber harvesting, and fire suppression. Today, the longleaf pine ecosystem is restricted to less than 5% of its original range, and ranks among the most endangered ecosystems in the United States (Noss et al. 1995, America's Longleaf 2009).

*email address: jskleinman@crimson.ua.edu Received September 15, 2017; Accepted April 11, 2018. Published: June 7, 2018.

DOI: 10.2179/17-148

The Oakmulgee District of the Talladega National Forest is the largest remnant of the longleaf pine ecosystem in Alabama (Figure 1). Located in the "longleaf pine hills" of central Alabama, the Oakmulgee District was largely spared from cultivation because it had steep slopes and infertile soils poorly suited for agriculture (Harper 1943). Although settlers utilized some longleaf pine for turpentine (Reed 1905), land-use change was most extreme ca. 1910–1930 corresponding to ownership by Kaul Lumber Company (Cox and Hart 2015). Industrial-scale timber harvesting on the Oakmulgee District ceased in 1931, and the land was federally acquired in 1935 (Cox and Hart 2015).

Most management on the Oakmulgee District is directed toward restoring longleaf pinedominated woodlands with open midstories and native ground cover plant communities. Restoration efforts include regeneration har-

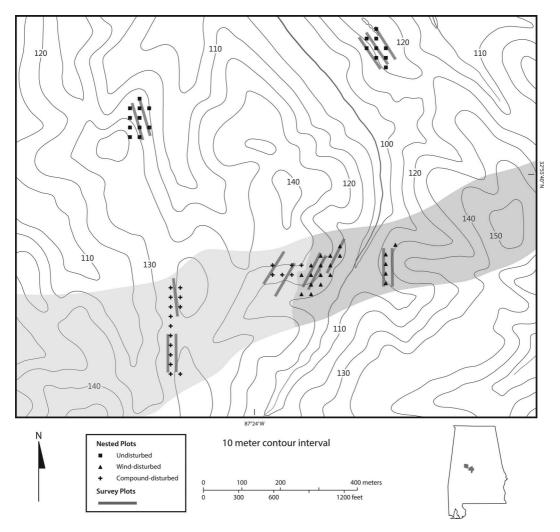


Figure 1. Map of the study area on the Oakmulgee District, Talladega National Forest, Alabama, USA. The 27 April 2011 EF3 tornado path is represented by light shading in compound-disturbed areas (wind-disturbed and salvage-harvested) and dark shading in unharvested wind-disturbed areas. Gray bars represent survey plots and symbols indicate the location of nested plots undisturbed (squares), wind-disturbed (triangles) and compound-disturbed (plus signs). The shaded area on the Alabama inset map represents the Oakmulgee District.

vests followed by site preparation and longleaf pine outplanting, density reductions in overstocked stands, and maintenance of a 2- to 5-yr prescribed fire rotation (USDA 2005). Among other desirable qualities, fire-maintained long-leaf pine ecosystems may support some of the most species-rich communities of native plants in temperate forests of North America (Walker and Silletti 2006).

With 135 vegetation associations corresponding to the longleaf pine ecosystem, successful restoration requires a comprehensive understanding of how plant composition changes across a broad range of environmental conditions (Peet 2006). Although regional surveys have been conducted (Harper 1943), and herbarium collections made available (Keener et al. 2017), only one floristic inventory on the Oakmulgee District has been published (Beckett and Golden 1982). Furthermore, limited information exists on the effects of natural distur-

bances and contemporary management practices on nonwoody plants.

On 27 April 2011, an EF3 tornado impacted the Oakmulgee District (National Weather Service [NWS] 2011). Salvage harvesting was conducted within seven months as a cost-effective strategy to mitigate risks of intense fire and insect outbreaks associated with wind-killed and weakened trees. Despite its utility, salvage harvesting may be criticized for further disrupting a recently disturbed system, and for removing natural disturbance legacies that facilitate recovery (Lindenmayer et al. 2004). For example, residual plants released by canopy removal may be damaged by salvage harvesting equipment, and plants that may otherwise recolonize winddisturbed sites may fail to establish where biomass removal and soil compaction result in unsuitable conditions.

Nonetheless, salvage harvesting operations vary by timing, extent, and severity, and a consensus has not been reached on the effects of post-wind disturbance salvage harvesting. Floristic response to natural disturbance and salvage harvesting typically corresponds most with the cumulative disturbance severity and timing of these events (Roberts 2004, Peterson and Leach 2008a). Rumbaitis del Rio (2006) attributed reduced herbaceous plant cover and diversity to post-wind disturbance salvage harvesting. However, Peterson and Leach (2008b) and Brewer et al. (2012) documented no such effects, in large part because of increased representation by early successional species on salvaged sites. More studies are needed to illustrate possible ecosystem responses to multiple disturbances of varying magnitudes across case-specific site conditions (Royo et al. 2016).

The purpose of this study was to document the effects of wind disturbance and salvage harvesting on the floristic composition of longleaf pine woodlands in the Alabama Fall Line Hills. Vascular plants were categorized by frequency of occurrence in areas undisturbed, wind-disturbed, and compound-disturbed (wind-disturbed and salvage-harvested). This floristic survey compliments Kleinman et al. (2017) who used multivariate analyses to relate differences in plant assemblages to variation in biophysical conditions on the same sites. The composition of plants documented in areas that experienced differential levels of disturbance may provide insight on taxon-specific life history traits and

responses to disturbance. Furthermore, the composition of plants documented may serve as a baseline to monitor recovery. With greater human demands and increased chances of high-severity natural disturbance events projected for the future, surveys such as this will be increasingly important to inform management actions in response to natural disturbances (Buma 2015, Seidl et al. 2017).

STUDY AREA This study took place in the Fall Line Hills, a physiographic transition belt spanning from Mississippi to Virginia (Fenneman 1938). Composed of the oldest marine-deposited sediments in the Coastal Plain, the Fall Line Hills have been deeply eroded by streams into steep slopes and ridges resembling the adjacent Appalachian Highlands. Soils in the Maubila series are common on hillslopes and ridges, and consist of a sandy loam or loam surface horizon up to 10 cm deep and clay-based substrata up to 200 cm deep to bedrock (USDA, NRCS 2017). Weathered from sediments in the Tuscaloosa Formation dating back to the Cretaceous period, Maubila series soils have a subangular blocky structure, are moderately well-drained, and have a high content of large ironstone fragments (USDA, NRCS 2008).

The climate of the region is humid mesothermal, characterized by a long, hot growing season and year-round precipitation (Thornthwaite 1948). The frost-free period spans ca. 230 days March–November (USDA, NRCS 2008). The average three-decade (1981–2010) temperature is 17°C annually, with the highest monthly average of 27°C in July and the lowest monthly average of 7°C in January (PRISM 2017). The average three-decade (1981–2010) precipitation is 1376 mm annually, with the highest monthly precipitation of 139 mm in February and the lowest monthly precipitation of 87 mm in October (PRISM 2017).

The Fall Line Hills ecoregion (level III) occurs within the broader Oak (*Quercus*)-Pine (*Pinus*) forest region of the United States (Braun 1950, Griffith et al. 2001). Beckett and Golden (1982) characterized eight forest community types within the same watershed as the study area. The Longleaf Pine type was the most common, occurring primarily on fire-maintained upper slopes, but also extending to lower slope positions with south-facing aspects. This community type corresponds to the US National Vegetation Classification association titled "Xe-

ric Upper East Gulf Coastal Plain Longleaf Pine Woodland" (Teague et al. 2014). The other community types characterized by Beckett and Golden (1982) were limited to lower slopes, steep north-facing slopes, mesic coves, and areas that had experienced intense timber harvesting. Although longleaf pine woodlands approach nearly monospecific canopy strata, a diversity of hardwoods and herbaceous species may grow in the understory (Harper 1943). Plant communities in the Fall Line Hills are particularly distinctive, because species typical of the Appalachian Highlands commonly co-occur with Coastal Plain species (Shankman and Hart 2007).

This study occurred on the northwest portion of the Oakmulgee District in Bibb County, Alabama. The EF3 tornado that tracked through the study area was one of 362 confirmed tornadoes that occurred during the 25–28 April 2011 Super Outbreak. The tornado had estimated wind speeds of 233 kph and a maximum width of 1609 m (NWS 2011). Wind-damaged trees of all species and size classes were made available by the Oakmulgee District for salvage harvesting July-November 2011 at the discretion of operators in designated areas. Salvage harvesting was concentrated near preexisting road networks where wheeled feller-bunchers and chainsaws were used to fell trees, and wheeled skidders were used to skid logs to ramp sites where they were loaded onto truck/trailer combinations with stationary knuckleboom loaders. Many wind-disturbed areas were left unharvested because of the surplus of salvageable wood generated by the 2011 Super Outbreak. The presence of areas undisturbed, wind-disturbed but unharvested, and compound-disturbed (wind-disturbed and salvage-harvested) provided the opportunity to compare the floristic composition of areas differentially affected by wind disturbance and salvage harvesting.

STUDY DESIGN To ascribe differences in floristic composition to the wind disturbance and salvage harvesting events, sites that shared analogous predisturbance conditions were selected. Satellite imagery, geospatial data from the USDA Forest Service, and ground reconnaissance were used to select sites that: (a) were longleaf pine dominated, (b) established before 1940, (c) shared upper and middle slope positions, (d) had Maubila series soils, (e) occurred within a 1 km² expanse, (f) occurred in the same watershed, and (g) occurred in the same Forest

Service-delineated compartment. Proximity in the same compartment ensured that the sites experienced the same contemporary prescribed fire regime, including fires in May 2010 and April 2014

Three disturbance categories (undisturbed, wind-disturbed, and compound-disturbed) were delineated within the selected sites. Undisturbed areas exhibited no visible tornado damage, and were assumed to represent predisturbance conditions using a space-for-time substitution. Although limited in explanatory power, this assumption was justified given the spatial proximity, shared biophysical site characteristics, and common management history of the selected sites (Pickett 1989). Care was taken to select undisturbed sites where the composition and structure of live trees resembled the dead and damaged trees on wind- and compounddisturbed sites. Wind-disturbed areas were directly impacted by the tornado, and compounddisturbed areas were wind-disturbed and salvage-harvested. Compound-disturbed areas exhibited obvious signs of salvage harvesting, including mechanically cut stems, which were not observed in wind-disturbed areas left unharvested.

Two plot designs (nested plots and survey plots) were used to examine the floristic composition of undisturbed, wind-disturbed, and compound-disturbed areas (Figure 1). The nested plot approach included 20 nested plots in each disturbance category (n = 60) that were sampled only once May-July 2016. Nested plots were systematically established with 25 m spacing. Each nested plot consisted of a 400-m² plot used to document the presence/absence of saplings and trees (woody plants > 1 m in height) and 10 nested 1×1 m quadrats (10 m²) used to document the presence/absence of ground flora (woody and herbaceous plants < 1 m in height). The survey plot approach included five 1000-m^2 plots $(10 \times 100 \text{ m})$ in each disturbance category (n = 15). Survey plots were established with long axes parallel to midslope, and were monitored every two weeks May-July 2016 for the presence/absence of all vascular plants. Unknown plants were collected, labeled by location, and transported to the lab to be pressed, dried, and identified. Voucher specimens were deposited at the University of Alabama Herbarium (UNA). With the exception of grasses (Poaceae), which were not identified beyond family, vascular plants were identified to genus or species given available reproductive structures (Radford et al. 1968, Miller and Miller 2005, Weakley 2015, Keener et al. 2017). Although taxonomic concepts varied across plant identification guides, all taxa were keyed using Weakley (2015), which served as our primary source of nomenclature.

Plants were assigned one of four frequency categories (rare, occasional, common, or abundant) in each disturbance category where they were documented. Rare plants included those that were documented in a survey plot and/or occurred on no more than one nested plot per disturbance category. Occasional plants occurred on 2-5 nested plots per disturbance category. Common plants occurred on 6-15 nested plots per disturbance category. Abundant plants occurred on 16-20 nested plots per disturbance category. Frequency rankings considered plants that were identified to species separately from plants that were only identified to genus. For example, heartleaf aster (Symphyotrichum cordifolium) and late purple aster (Symphyotrichum patens) were each ranked individually and separately from the genus Symphyotrichum, which may have included white bushy aster (Symphyotrichum dumosum (L.) G.L.Nesom) and Short's aster (Symphyotrichum shortii (Lindl.) G.L.Nesom), among other Symphyotrichum species.

RESULTS AND DISCUSSION The 2011 tornado and salvage harvesting operation had noticeable impacts on the vascular plant composition of longleaf pine woodlands of the Oakmulgee District. A floristic inventory conducted May-July 2016 documented 192 plant taxa representing 68 families and 137 genera (Table 1). Overall, 68 plant taxa were common to all disturbance categories. Undisturbed areas contained 90 plant taxa, of which 9 were unique; wind-disturbed areas contained 160 plant taxa, of which 48 were unique; and compounddisturbed areas contained 126 plant taxa, of which 19 were unique. Thus, using a space-fortime substitution, we attributed increased taxonomic richness to the wind event, and reduced taxonomic richness to salvage harvesting. Nonetheless, each disturbance category had unique plants that contributed to overall taxonomic richness.

Consistent with Beckett and Golden (1982), the composite flower family (Asteraceae) exhibited the greatest taxonomic richness with 37 taxa. The legume family (Fabaceae) was the next most diverse with 17 taxa. Native legumes are capable of fixing atmospheric nitrogen, and help maintain nitrogen balance in fire-maintained longleaf pine ecosystems (Cathey et al. 2010). Virginia goat's rue (*Tephrosia virginiana*), a native legume, was particularly widespread, occurring on 70% of nested plots in undisturbed areas, 55% of nested plots in wind-disturbed areas, and 95% of nested plots in compound-disturbed areas.

The beech family (Fagaceae) was the third most diverse family with 16 taxa. Thirteen of the 16 taxa were oaks (Quercus), which comprised the most species-rich genus in the study area. The composition of oaks exemplified plant communities in the Fall Line Hills, representing species from the Coastal Plain and Appalachian Highlands. For example, sand post oak (Quercus margarettae) is primarily Coastal, and was documented on three nested plots with rock chestnut oak (Quercus montana), which is primarily Appalachian (Weakley 2015). Although traditional longleaf pine management often involves prescriptions to reduce the component of oaks, many oaks are becoming increasingly valued for pyrophytic qualities and wildlife uses in the longleaf pine ecosystem (Hiers et al. 2014). Moreover, oaks may facilitate the establishment of longleaf pine seedlings, thereby promoting the recovery of longleaf pine following catastrophic canopy removal (Loudermilk et al. 2016).

Undisturbed sites had the fewest plant taxa overall and the fewest unique plant taxa compared to wind- and compound-disturbed sites. With the exception of dwarf iris (Iris verna), which was documented on two nested plots (10%), the other eight unique species on undisturbed sites were categorized as rare. Therefore, if the plant composition documented on undisturbed sites represents a reference condition for the recovered state of wind- and compounddisturbed sites, then disturbed sites need few plants to recolonize to achieve a comparable state of succession. Nonetheless, comparing the presence/absence of rare taxa across disturbance categories may provide an incomplete assessment of recovery, as more frequent taxa typically contribute more to collective ecosystem processes (Díaz et al. 2006).

Leech brush (Nestronia umbellula) and American chestnut (Castanea dentata) were notewor-

Table 1. Vascular plants documented May–July 2016 in undisturbed (UND), wind-disturbed (WIND), and compound-disturbed (COMP) longleaf pine woodlands of the Oakmulgee District, Talladega National Forest, Alabama, USA. Plants are ranked by frequency in each disturbance category where they were documented. Rare plants (R) were only documented in a survey plot and/or occurred on no more than one nested plot per disturbance category (<10%). Occasional plants (O) occurred on 2–5 nested plots per disturbance category (30–75%). Common plants (C) occurred on 6–15 nested plots per disturbance category (30–75%). Abundant plants (A) occurred on 16–20 nested plots per disturbance category (80–100%). Voucher specimens are parenthetically indicated with a "V" and collection number. All vouchers were collected by Jonathan Kleinman and were deposited at the University of Alabama Herbarium (UNA).

Family	Taxon	UND	WIND	COMP
ACANTHACEAE	Ruellia caroliniensis (J.F.Gmel.) Steud.		R	
AGAVACEAE	Yucca filamentosa L.		O	O
ALTINGIACEAE	Liquidambar styraciflua L.	\mathbf{C}	A	$^{\rm C}$
ANACARDIACEAE	Toxicodendron pubescens Mill.	R	R	R
	Toxicodendron radicans (L.) Kuntze	\mathbf{C}	O	O
	Rhus copallinum L.	\mathbf{C}	A	A
	Rhus glabra L.		\mathbf{C}	R
ANNONACEAE	Asimina parviflora (Michx.) Dunal	O	O	O
APIACEAE	Angelica venenosa (Greenway) Fernald		R	R
	Eryngium yuccifolium Michx. (V1)	O		R
APOCYNACEAE	Asclepias tuberosa L.	R	R	R
	Asclepias variegata L.			R
AQUIFOLIACEAE	Ilex opaca Aiton			R
ARISTOLOCHIACEAE	Hexastylis arifolia (Michx.) Small		R	
ASTERACEAE	Ageratina aromatica (L.) Spach		R	R
	Ambrosia artemisiifolia L.			R
	Arnoglossum atriplicifolium (L.) H.Rob.		R	
	Chrysopsis mariana (L.) Elliott	R	R	O
	Cirsium Mill.		R	R
	Conoclinium coelestinum (L.) DC.		R	R
	Conyza canadensis (L.) Cronquist		A	C
	Coreopsis auriculata L.		R	
	Coreopsis major Walter	\mathbf{C}	C	A
	Elephantopus tomentosus L.	Ö	R	R
	Erechtites hieraciifolius (L.) Raf. ex DC.	0	R	10
	Erigeron strigosus Muhl. ex Willd. (V2)		10	R
	Eupatorium album L.	R	R	R
	Eupatorium capillifolium (Lam.) Small	It	0	R
	Eupatorium hyssopifolium L.		O	R R
		О	C	n O
	Eupatorium rotundifolium L.	U	C	0
	Gamochaeta argyrinea G.L.Nesom			U
	Helianthus hirsutus Raf.		R	0
	Hieracium gronovii L.		0	O
	Krigia Schreb.		R	0
	Lactuca canadensis L.		A	О
	Liatris Schreb.	O	R	
	Nabalus Cass.		R	
	Packera anonyma (Wood) W.A.Weber & A.Löve	0	R	a
	Pityopsis graminifolia (Michx.) Nutt.	C	С	C
	Pseudognaphalium helleri (Britton) Anderb.		R	O
	Pseudognaphalium obtusifolium (L.) Hilliard & Burtt		0	R
	Rudbeckia hirta L.		R	
	Sericocarpus linifolius (L.) Britton, Sterns, & Poggenb. (V3)	0	R	O
	Sericocarpus tortifolius (Michx.) Nees	C	C	C
	Solidago odora Aiton	A	A	C
	Symphyotrichum Nees	C	A	C
	Symphyotrichum cordifolium (L.) G.L.Nesom		O	
	Symphyotrichum patens (Aiton) G.L Nesom	O	R	R
	Trilisa odoratissima (J.F.Gmel.) Cass.	R	R	R
	Vernonia angustifolia Michx.	O	R	O
BLECHNACEAE	Lorinseria areolata (L.) C.Presl (V4)		O	
CAMPANULACEAE	Lobelia puberula Michx.		R	R
	Triodanis Raf.			R

Table 1. Continued

Family	Taxon	UND	WIND	COMP
CANNABACEAE	Celtis laevigata Willd.		R	R
CARYOPHYLLACEAE	Silene virginica L.		R	
COMMELINACEAE	Tradescantia ohiensis Raf.			R
	Tradescantia subaspera Ker Gawl.		R	
CONVOLVULACEAE	Calystegia catesbeiana Pursh (V6)		O	R
	Ipomoea pandurata (L.) G.Mey.		R	
	Stylisma humistrata (Walter) Chapm.		R	O
CORNACEAE	Cornus florida L.	C	O	C
CUPRESSACEAE	Juniperus virginiana L.			R
CYPERACEAE	Rhynchospora globularis (Chapm.) Small		R	
011 214102122	Scirpus atrovirens Willd.			R
	Scleria triglomerata Michx.	O	0	0
DENNSTAEDTIACEAE	Pteridium latiusculum (Desv.) Hieron.	Č	Č	Č
DEIWIGHTED THE CELL	ex R.E.Fr. = {syn: P. aquilinum}	C	C	C
DIOSCOREACEAE	Dioscorea villosa L.		R	
DRYOPTERIDACEAE	Polystichum acrostichoides (Michx.) Schott		R	
EBENACEAE	Diospyros virginiana L.	A	A	A
ERICACEAE	Epigaea repens L. (V7)	R	R	R
Пислопи	Gaylussacia dumosa (Andrews) Torr. & A.Gray	C	R	C
	Oxydendrum arboreum (L.) DC.	C	A	C
	Rhododendron canescens (Michx.) Sweet	C	R	O
	Vaccinium arboreum Marshall	Α	A	A
	Vaccinium elliottii Chapm.	0	0	R
	Vaccinium pallidum Aiton	O	Ö	11
	Vaccinium stamineum L.	0	C	0
EUPHORBIACEAE	Acalypha gracilens A. Gray	R	C	R
EUFHORDIACEAE	Cnidoscolus stimulosus (Michx.) Engelm. & A.Gray (V5)	R R	R	ĸ
	Euphorbia pubentissima Michx.	C	C	C
	Stillingia sylvatica Garden ex L.	R	C	C
	ŭ ŭ		C	C
	Tragia smallii Shinners	C R	C R	R
	Tragia urens L.	ĸ		ĸ
ELE LOBLE	Tragia urticifolia Michx.	D	R	
FABACEAE	Centrosema virginianum (L.) Benth.	R	R	ъ
	Chamaecrista fasciculata (Michx.) Greene	0	0	R
	Clitoria mariana L.	O	0	ъ
	Crotalaria sagittalis L. (V8)		0	R
	Desmodium laevigatum (Nutt.) DC.		R	
	Desmodium viridiflorum (L.) DC.	ъ	R	
	Galactia erecta (Walter) Vail	R	_	
	Galactia volubilis (L.) Britton var. volubilis	_	R	
	Lespedeza hirta (L.) Hornem.	O	R	
	Lespedeza procumbens Michx.	_	R	_
	Lespedeza repens (L.) W.Barton	O	O	O
	Lespedeza violacea (L.) Pers.		O	R
	Mimosa microphylla Dryand.	O	O	R
	Rhynchosia reniformis DC.	R		
	Rhynchosia tomentosa (L.) Hook. & Arn.		R	
	Stylosanthes biflora (L.) Britton, Sterns, & Poggenb.	O	O	O
	Tephrosia virginiana (L.) Pers.	\mathbf{C}	\mathbf{C}	A

Table 1. Continued

Family	Taxon	UND	WIND	COMP
FAGACEAE	Castanea dentata (Marshall) Borkh.	R		
	Castanea pumila (L.) Mill.	O		O
	Fagus grandifolia Ehrh.		\mathbf{R}	
	Quercus alba L.	C	A	\mathbf{C}
	Quercus coccinea Münchh.	C	A	C
	Quercus falcata Michx.	C	A	A
	Quercus hemisphaerica Bartram ex Willd.	O	\mathbf{C}	C
	Quercus laevis Walter	C	\mathbf{C}	$^{\mathrm{C}}$
	Quercus incana Bartram	O	O	$^{\mathrm{C}}$
	Quercus margarettae W.W. Ashe ex Small	O	\mathbf{C}	$^{\mathrm{C}}$
	Quercus marilandica Münchh. var. marilandica	C	\mathbf{C}	Α
	Quercus montana Willd.		C	R
	Quercus nigra L.	C	A	Α
	Quercus rubra L.	O	O	O
	Quercus stellata Wangenh.	C	\mathbf{C}	A
	Quercus velutina Lam.	C	A	\mathbf{C}
GELSEMIACEAE	Gelsemium sempervirens (L.) StHil.	A	A	A
HAMAMELIDACEAE	Hamamelis virginiana L.		O	R
HYDRANGEACEAE	Hydrangea arborescens L.		\mathbf{R}	
	Hydrangea quercifolia Bartram	R		
HYPERICACEAE	Hypericum hypericoides (L.) Crantz	C	O	\mathbf{C}
	Hypericum gentianoides (L.) Britton, Sterns, & Poggenb.	R	O	\mathbf{C}
IRIDACEAE	Iris verna L.	O		
JUGLANDACEAE	Carya glabra (Mill.) Sweet	O	A	O
	Carya tomentosa (Lam.) Nutt.	C	A	$^{\mathrm{C}}$
LAMIACEAE	Callicarpa americana L.	C	O	O
	Scutellaria elliptica Muhl. ex Spreng. var. elliptica		O	
LAURACEAE	Sassafras albidum (Nutt.) Nees	C	\mathbf{C}	O
LILIACEAE	Lilium michauxii Poir.		\mathbf{R}	
LINACEAE	Linum virginianum L.			R
MAGNOLIACEAE	Liriodendron tulipifera L.	R	О	R
	Magnolia macrophylla Michx.		О	R
	Magnolia virginiana L.			R
MELASTOMATACEAE	Rhexia mariana L. var. mariana		\mathbf{R}	
	Rhexia virginica L.		\mathbf{R}	R
MYRICACEAE	Morella caroliniensis (Mill.) Small			R
NARTHECIACEAE	Aletris farinosa L. (V9)		R	
NYSSACEAE	Nyssa sylvatica Marshall	C	С	C
ONAGRACEAE	Oenothera filipes (Spach) W.L.Wagner & Hoch		\mathbf{R}	
OROBANCHACEAE	Agalinis purpurea (L.) Pennell	O	О	A
	Aureolaria flava (L.) Farw.		R	_
	Aureolaria pectinata (Nutt.) Pennell			R
OSMUNDACEAE	Osmundastrum cinnamomeum (L.) C.Presl		O	R
	Osmunda spectabilis Willd.	_	R	R
OXALIDACEAE	Oxalis L.	R	O	
PASSIFLORACEAE	Passiflora lutea L.		R	
PHYTOLACCACEAE	Phytolacca americana L.	_	O	
PINACEAE	Pinus echinata Mill.	О	О	
	Pinus palustris Mill.	A	С	A
	Pinus taeda L.	A	С	A
PLANTAGINACEAE	Veronica arvensis L.			R
POACEAE		A	A	A
POLEMONIACEAE	Phlox pilosa L.		R	
POLYGALACEAE	Persicaria Mill.		R	
	Polygala nana (Michx.) DC.	R		R
	Polygala polygama Walter			R
	Polygonum L.		R	
RHAMNACEAE	Berchemia scandens (Hill) K.Koch		R	R

Table 1. Continued

Family	Taxon	UND	WIND	COMP
ROSACEAE	Amelanchier arborea (F.Michx.) Fernald	R		
	Aronia arbutifolia (L.) Pers.		R	R
	Potentilla simplex Michx.		R	
	Prunus alabamensis C.Mohr			R
	Prunus serotina Ehrh. var. serotina		O	R
	Prunus umbellata Elliott		O	O
	Rubus L.	O	\mathbf{C}	\mathbf{C}
RUBIACEAE	Diodella teres (Walter) Small		R	C
	Galium pilosum Aiton	R	R	
	Houstonia caerulea L.	R	O	
	Mitchella repens L.		R	
SANTALACEAE	Nestronia umbellula Raf. (V10)	R		
SAPINDACEAE	Acer floridanum (Chapm.) Pax		O	
	Acer rubrum L.	\mathbf{C}	C	C
	Acer saccharum Marshall		R	
	Aesculus pavia L. var. pavia		R	
SAPOTACEAE	Sideroxylon lanuginosum Michx. ssp.		R	
	lanuginosum (V11)			
SMILACACEAE	Smilax bona-nox L.	\mathbf{C}	O	C
	Smilax glauca Walter	A	A	A
	Smilax pumila Walter		R	
	Smilax rotundifolia L.	C	C	O
	Smilax smallii Morong		Ō	R
SOLANACEAE	Physalis longifolia Nutt. var. subglabrata			R
	(Mack. & Bush) Cronquist			
STYRACACEAE	Styrax grandifolius Aiton		C	O
SYMPLOCACEAE	Symplocos tinctoria (L.) L'Hér.		Č	Ō
TETRACHONDRACEAE	Polypremum procumbens L.			R
ULMACEAE	Ulmus americana L.		R	
VIOLACEAE	Viola brittoniana Pollard	R		
	Viola pedata L.	0	O	O
VITACEAE	Muscadinia rotundifolia (Michx.) Small	Č	Ā	Č
	Parthenocissus quinquefolia (L.) Planch.		0	R
	Vitis aestivalis Michx. var. aestivalis		R	R
XYRIDACEAE	Xyris L.		R	

thy species with single nested plot occurrences on undisturbed sites. Leech brush, which is threatened by intensive timber production and habitat fragmentation that limit gene flow between clonal populations (NatureServe 2017), is listed as imperiled (S2) in Alabama (Alabama Natural Heritage Program [ALNHP] 2017). American Chestnut trees were once widespread in the eastern United States, with a southern range extending to central Alabama prior to functional extinction by the fungal pathogen Cryphonectria parasitica (Murrill) Barr in the early 20th century (Russell 1987). At the time of his survey, Reed (1905) documented only one "perfect specimen" of American chestnut among many "dead stubs" scattered throughout the presentday boundaries of the Oakmulgee District. Beckett and Golden (1982) also described the rare occurrence of American chestnut, which was likely reduced to small stature as documented in our survey.

The wind event clearly facilitated increased taxonomic richness in the study area. Consistent with trends observed on undisturbed sites, 42 of the 48 unique taxa documented on wind-disturbed sites were categorized as rare (the other six were occasional). Increased taxonomic richness of plants was attributed to increased resource availability and heterogeneity of microclimatic conditions (Swanson et al. 2011). Specifically, wind-induced canopy removal increased light availability, bare mineral soil exposure, and deposition of woody material on the forest floor (Kleinman et al. 2017). Accumulation of downed woody debris and dense clusters of saplings may have influenced microsite moisture conditions. Thus, the wind event generated a matrix of damp, shaded microsites

among dry, exposed areas that collectively enabled coexistence of a diversity of plant taxa with different habitat requirements.

Reduced taxonomic richness on compounddisturbed sites compared to wind-disturbed sites was attributed to salvage-harvest mediated habitat homogenization and reduction in resource availability. Specifically, the volume of coarse woody debris was significantly reduced from wind- to compound-disturbed sites, which may have limited the input of decompositionderived nutrients and availability of microsites associated with build-up around coarse woody debris (Kleinman et al. 2017). Although not quantified in the present study, salvage harvesting equipment may compact soil, thereby reducing soil permeability, water holding capacity, and oxygen availability (Cambi et al. 2015). Indeed, we observed a patch ca. 300 m² in size that was almost completely devoid of an organic surface layer where heavy machinery was likely concentrated during the salvage harvesting operation.

Despite noticeable desiccation on compounddisturbed sites, two of the unique taxa documented are often associated with moist habitat: sweet bay magnolia (Magnolia virginiana) and black bulrush (Scirpus atrovirens). These and the other unique taxa on compound-disturbed sites were categorized as rare, warranting caution in characterizing site conditions based on the occurrence of rare species. However, the other unique taxa were more characteristic of disturbed areas, including common ragweed (Ambrosia artemisiifolia), juniper leaf (Polypremum procumbens), common partridge pea (Chamaecrista fasciculata), and corn speedwell (Veronica arvensis). Notably, corn speedwell, a native of Eurasia, was the only nonnative plant documented in the study area (Weakley 2015). Nonetheless, the single documented corn speedwell occurrence certainly did not pose a threat of invasion.

Absence of nonnative invasive plants in the study area was unexpected because disturbances, especially salvage harvesting, are often associated with colonization by invasive plants (Brewer et al. 2012). Although grasses were not distinguished beyond family, we are confident that invasive grasses such as cogon grass (*Imperata cylindrica* (L.) P. Beauv.) and Japanese stilt grass (*Microstegium vimineum* (Trin.) A. Camus) were absent. Other nonnative inva-

sive species that occur on the Oakmulgee District such as Japanese climbing fern (*Lygodium japonicum* (Thunb.) Sw.), Chinese privet (*Ligustrum sinense* Lour.), and sericea lespedeza (*Lespedeza cuneata* G. Don) were also absent. Interestingly, sericea lespedeza was documented by Kleinman and Hart (2017) on a proximal site with similar biophysical characteristics that experienced an unusually long period of fire exclusion. Thus, absence of nonnative invasive plants in this study may be explained in part by the regular occurrence of prescribed fire (Sorrie et al. 2006).

Plant assemblages in the longleaf pine ecosystem are largely impacted by fires, which fluctuate by intensity and spatial extent with variation in the abundance, composition, and distribution of fuels (Mitchell et al. 2006). Although the prescribed fire in May 2010 likely behaved consistently across the study area, modified fuel configurations following the 2011 disturbance events likely caused the April 2014 prescribed fire to differentially impact residual vegetation across disturbance categories. As such, observed differences in the floristic composition across disturbance categories may be explained further by the interaction of undisturbed, wind-disturbed, and compound-disturbed sites with the background disturbance of prescribed fire. Although fire effects were not explicitly quantified in this study, the composition of species documented may provide insight on the interacting effects of wind disturbance, salvage harvesting, and prescribed fire in other firemaintained systems.

This study adds to a limited body of literature on the effects of post-wind-disturbance salvage harvesting. We documented a clear reduction in taxonomic richness from wind- to compounddisturbed sites that was attributed primarily to salvage harvesting. Despite this reduction, compound-disturbed sites had a greater taxonomic richness of plants than undisturbed sites. Furthermore, most plants that were unique to a particular disturbance category were rare (documented on <10% of nested plots). Decisions on whether to salvage harvest must consider the ecological significance of these rare plants in early stages of succession, and consider if salvage harvesting has long-term impacts on post-wind-disturbance recovery. Although this study was limited in part by a relatively short time since the disturbance events and a relatively short period of data collection, the floristic inventory presented here provides the baseline to monitor recovery on the Oakmulgee District. Furthermore, the composition of plants documented provides insight on the short-term responses of vascular plants to interacting disturbances in an understudied region of the endangered longleaf pine ecosystem.

ACKNOWLEDGMENTS Thanks go to Scott Ford for helping design and implement the study; Carson Barefoot and Jonathan Davis Goode for assistance in the field and lab; the U.S.D.A. Forest Service, Oakmulgee District for logistical support and funding; Brian Keener for plant identification assistance; and Woodward S. Bousquet and two anonymous reviewers for comments that greatly improved the final manuscript.

LITERATURE CITED

- Alabama Natural Heritage Program (ALNHP). 2017. Alabama inventory list: the rare, threatened and endangered plants and animals of Alabama. Alabama Natural Heritage Program, Auburn University, Alabama.
- America's Longleaf. 2009. Range-wide conservation plan for longleaf pine (www.americaslongleaf. org/resources/conservation-plan, 5 September 2017). Regional Working Group for America's Longleaf.
- Beckett, S. and M.S. Golden. 1982. Forest vegetation and vascular flora of Reed Brake Research Natural Area, Alabama. Castanea 47: 368–392.
- Braun, E.L. 1950. Eastern deciduous forests of North America. The Blackburn Press, Caldwell, New Jersey.
- Brewer, J.S., C.A. Bertz, J.B. Cannon, J.D. Chesser, and E.E. Maynard. 2012. Do natural disturbances or the forestry practices that follow them convert forests to early-successional communities? Ecol. Applic. 22:442–458.
- Buma, B. 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. Ecosphere 6:1–15.
- Cambi, M., G. Certini, F. Neri, and E. Marchi. 2015. The impact of heavy traffic on forest soils: a review. Forest Ecol. Managem. 338: 124–138.

- Cathey, S.E., L.R. Boring, and T.R. Sinclair. 2010. Assessment of N_2 fixation capability of native legumes from the longleaf pine-wiregrass ecosystem. Environmental and Experimental Botany 67:444–450.
- Cox, L.E. and J.L. Hart. 2015. Two centuries of forest compositional and structural changes in the Alabama Fall Line Hills. Amer. Midl. Naturalist 174:218–237.
- Díaz, S., J. Fargione, F.S. Chapin III, and D. Tilman. 2006. Biodiversity loss threatens human well-being. PLoS Biol. 4:e277.
- Fenneman, N.M. 1938. Physiography of the eastern United States. McGraw-Hill, New York, New York.
- Frost, C.C. 2006. History and future of the longleaf pine ecosystem. p. 9–42. *In*: Jose, S., E.J. Jokela, and D.L. Miller (eds.). The longleaf pine ecosystem: Ecology, silviculture, and restoration. Springer, New York, New York.
- Griffith, G.E., J.M. Omernik, J.A. Comstock, S. Lawrence, G. Martin, A. Goddard, V.J. Hulcher, and T. Foster. 2001. Ecoregions of Alabama and Georgia (Color Poster with Map, Descriptive Text, Summary Tables, and Photographs; Map Scale 1:17,000,000). U.S. Geological Survey, Reston, Virginia.
- Harper, R.M. 1943. Forests of Alabama. Geological Survey of Alabama, Monograph 10. Wetumpka Printing Company, Wetumpka, Alabama.
- Hiers, J.K., J.R. Walters, R.J. Mitchell, J.M. Varner, L.M. Conner, L.A. Blanc, and J. Stowe. 2014. Ecological value of retaining pyrophytic oaks in longleaf pine ecosystems. J. Wildlife Managem. 78:383–393.
- Keener, B.R., A.R. Diamond, L.J. Davenport, P.G. Davison, S.L. Ginzbarg, C.J. Hansen, C.S. Major, D.D. Spaulding, J.K. Triplett, and M. Woods. 2017. Alabama Plant Atlas. [S.M. Landry and K.N. Campbell (original application development), Florida Center for Community Design and Research. University of South Florida]. University of West Alabama, Livingston, Alabama.
- Kleinman, J.S. and J.L. Hart. 2017. Response by vertical strata to catastrophic wind in restored *Pinus palustris* stands. Bull. Torrey Bot. Soc. 144:423–438.

- Kleinman, J.S., S.A. Ford, and J.L. Hart. 2017. Catastrophic wind and salvage harvesting effects on woodland plants. Forest Ecol. Managem. 403:112–125.
- Lindenmayer, D.B., D.R. Foster, J.F. Franklin, M.L. Hunter, R.F. Noss, F.A. Schmiegelow, and D. Perry. 2004. Salvage harvesting policies after natural disturbance. Science 303:1303.
- Loudermilk, E.L., J.K. Hiers, S. Pokswinski, J.J. O'Brien, A. Barnett, and R.J. Mitchell. 2016. The path back: oaks (*Quercus* spp.) facilitate longleaf pine (*Pinus palustris*) seedling establishment in xeric sites. Ecosphere. 7:1–14.
- Miller, J.H. and K.V. Miller. 2005. Forest plants of the Southeast and their wildlife uses, revised ed., University of Georgia Press, Athens, Georgia.
- Mitchell, R.J., J.K. Hiers, J.J. O'Brien, S.B. Jack, and R.T. Engstrom. 2006. Silviculture that sustains: the nexus between silviculture, frequent prescribed fire, and conservation of biodiversity in longleaf pine forests of the southeastern United States. Canad. J. Forest Res. 36:2724–2736.
- NatureServe. 2017. NatureServe Explorer: An online encyclopedia of life Version 7.1. (http://explorer.natureserve.org, 20 August 2017). NatureServe, Arlington, Virginia.
- Noss, R.F., E.T. LaRoe III, and J.M. Scott. 1995. Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. Biological Report 28. USDI National Biological Service, Washington, D.C.
- National Weather Service (NWS). 2011. Sawyer-ville-Eoline (Greene, Hale, and Bibb Counties) EF-3 tornado April 27 2011. (https://www.weather.gov/bmx/event_04272011sawyerville, 20 November, 2016). NWS Weather Forecast Office, Birmingham, Alabama.
- Peet, R.K. 2006. Ecological classification of longleaf pine woodlands. p. 51–93. *In*: Jose, S., E.J. Jokela, and D.L. Miller (eds.). The longleaf pine ecosystem: Ecology, silviculture, and restoration. Springer, New York, New York.
- Peterson, C.J. and A.D. Leach. 2008a. Limited salvage logging effects on forest regeneration after moderate-severity windthrow. Ecol. Applic. 18:407–420.

- Peterson, C.J. and A.D. Leach. 2008b. Salvage logging after windthrow alters microsite diversity, abundance and environment, but not vegetation. Forestry 81:361–376.
- Pickett, S.T.A. 1989. Space-for-time substitution as an alternative to long-term studies. p. 110–135. *In*: Likens, G.E. (ed.). Long-term studies in ecology: Approaches and alternatives. Springer-Verlag, New York, New York.
- PRISM Climate Group. 2017. Data explorer: Time series values for individual locations. (http://prism.oregonstate.edu/explorer/, 5 September 2017). Northwest Alliance for Computational Science and Engineering, Oregon State University, Corvallis, Oregon.
- Radford, A.E., H.E. Ahles, and C.R. Bell. 1968. Manual of the vascular flora of the Carolinas. University of North Carolina Press, Chapel Hill, North Carolina.
- Reed, F.W. 1905. A working plan for forest lands in central Alabama. USDA Forest Service, Bulletin 68, Government Printing Office, Washington, D.C.
- Roberts, M.R. 2004. Response of the herbaceous layer to natural disturbance in North American forests. Canad. J. Bot. 82:1273–1283.
- Royo, A.A., C.J. Peterson, J.S. Stanovick, and W.P. Carson. 2016. Evaluating the ecological impacts of salvage logging: can natural and anthropogenic disturbances promote coexistence? Ecology 97:1566–1582.
- Rumbaitis del Rio, C.M. 2006. Changes in understory composition following catastrophic windthrow and salvage logging in a subalpine forest ecosystem. Canad. J. Forest Res. 36:2943–2954.
- Russell, E.W. 1987. Pre-blight distribution of *Castanea dentata* (Marsh.) Borkh. Bull. Torrey Bot. Club 114:183–190.
- Seidl, R., D. Thom, M. Kautz, D. Martin-Benito, M. Peltoniemi, G. Vacchiano, J. Wild, D. Ascoli, M. Petr, J. Honkaniemi, M. Lexer, V. Trotsiuk, P. Mairota, M. Svoboda, M. Fabrika, T.A. Nagel, and C.P.O. Reyer. 2017. Forest disturbances under climate change. Nature Climate Change. 7:395–402.
- Shankman, D. and J.L. Hart. 2007. The fall line: a physiographic-forest vegetation boundary. Geogr. Rev. 97:502–519.

- Sorrie, B.A., J.D. Gray, and P.J. Crutchfield. 2006. The vascular flora of the longleaf pine ecosystem of Fort Bragg and Weymouth Woods, North Carolina. Castanea 71:129–161.
- Swanson, M.E., J.F. Franklin, R.L. Beschta, C.M. Crisafulli, D.A. DellaSala, R.L. Hutto, D.B. Lindenmayer, and F.J. Swanson. 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment 9:117–125.
- Teague, J., K.A. Palmquist, R.K. Peet, and S. Carr. 2014. Pinus palustris / Schizachyrium scoparium-Pteridium aquilinum Woodland [Version Date: November 7, 2014]. United States National Vegetation Classification. Federal Geographic Data Committee, Washington, D.C.
- Thornthwaite, C.W. 1948. An approach toward rational classification of climate. Geogr. Rev. 38:55–94.
- USDA, Forest Service. 2005. Longleaf Ecosystem Restoration Project. Final Environmental Impact Statement, National Forests in Alabama, Talladega National Forest, Oakmulgee District.

- United Stated Department of Agriculture, Natural Resources Conservation Service (USDA, NRCS). 2008. Soil Survey of Bibb County, Alabama (https://www.nrcs.usda.gov/Internet/FSE_MANUSCRIPTS/alabama/AL007/0/Bibb.pdf, 10 May 2018).
- United States Department of Agriculture, Natural Resources Conservation Service (USDA, NRCS). 2017. Web Soil Survey (http://websoilsurvey.nrcs.usda.gov/, 5 September 2017).
- Walker, J.L. and A.M. Silletti. 2006. Restoring the ground layer of longleaf pine ecosystems. p. 297–325. *In*: Jose, S., E.J. Jokela, and D.L. Miller (eds.). The longleaf pine ecosystem: Ecology, silviculture, and restoration. Springer, New York, New York.
- Weakley, A.S. 2015. Flora of the southern and mid-Atlantic states. Working draft of 21 May 2015. (http://www.herbarium.unc.edu/Flora Archives/WeakleyFlora_2015-05-29.pdf, 12 February 2018). University of North Carolina, North Carolina Botanical Garden, Chapel Hill, North Carolina.