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Woody Regeneration in a Southern Appalachian *Quercus* Stand Following Wind Disturbance and Salvage Logging

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ABSTRACT In the eastern United States, the practice of salvage logging is common to reclaim economic losses and/or reduce fuel loading following a natural disturbance. A current hypothesis states that two disturbances in rapid succession (i.e., compounded disturbance) have a cumulative severity of impact and may displace the successional trajectory further than either disturbance occurring separately. On 20 April 2011, Bankhead National Forest in Alabama was affected by an EF1 tornado with accompanying straight-line winds. Much of the damage was salvaged, however adjacent disturbance in a Wilderness Area was not harvested. A unique set of conditions allowed for comparisons of woody regeneration within a single stand, reducing uncontrolled variables to test the compounded disturbance hypothesis at a fine spatial scale. After two growing seasons, species richness, species evenness, and Shannon diversity of seedlings and saplings did not significantly differ by disturbance class. We found seedling density significantly differed between functional groups and we noted a significant interaction between functional groups and disturbance classes. In the sapling layer, density was significantly different among functional groups and among disturbance classes, but our results did not reveal a significant interaction between these factors. The wind disturbance accelerated succession in the *Quercus* stand toward dominance by shade-tolerant species, notably *A. rubrum*, and the salvage operation amplified the *Quercus*-to-*Acer* transition. However, even in wind-disturbed areas that were not salvaged, the regeneration model predicted *A. rubrum* to have more than twice the density of all combined *Quercus* species in the future stand.
Key words: *Acer rubrum*, compounded disturbance, *Quercus*, regeneration, salvage logging.

INTRODUCTION A compositional dichotomy exists between canopy and regeneration layers of most *Quercus* stands in the Central Hardwood Region of the eastern United States; the canopy is dominated by various *Quercus* species, whereas the midstory and regeneration layers are composed primarily of *Acer rubrum* and other shade-tolerant mesophytes (Lorimer 1984, Abrams 1998, Abrams 2003, Fei and Steiner 2009). Researchers have concluded that a pervasive and possibly unavoidable reduction of *Quercus* dominance across this region concomitant with an increase in the dominance of shade-tolerant species, such as *A. rubrum*, is imminent (Lorimer 1984, Abrams 2005, Nowacki and Abrams 2008, Fei et al. 2011). Several mechanisms contributing to this transition (i.e., the *Quercus*-to-*Acer* phenomenon) have been recognized including fire suppression, loss of *Castanea dentata* (Marsh.) Borkh., climate change, and Euro-American land-use change, among others (Abrams 1992, Hart et al. 2008, McEwan et al. 2011). A disturbance event, whether natural or anthropogenic, occurring during the understory reinitiation stage of development (Oliver and Larson 1996) has been found to promote this shift in species composition (Abrams and Scott 1989, Abrams and Nowacki 1992). Although singular disturbance events have been shown to facilitate this pattern, it is unknown how this successional trajectory is impacted by multiple disturbance episodes occurring in quick succession. The compounded disturbance hypothesis

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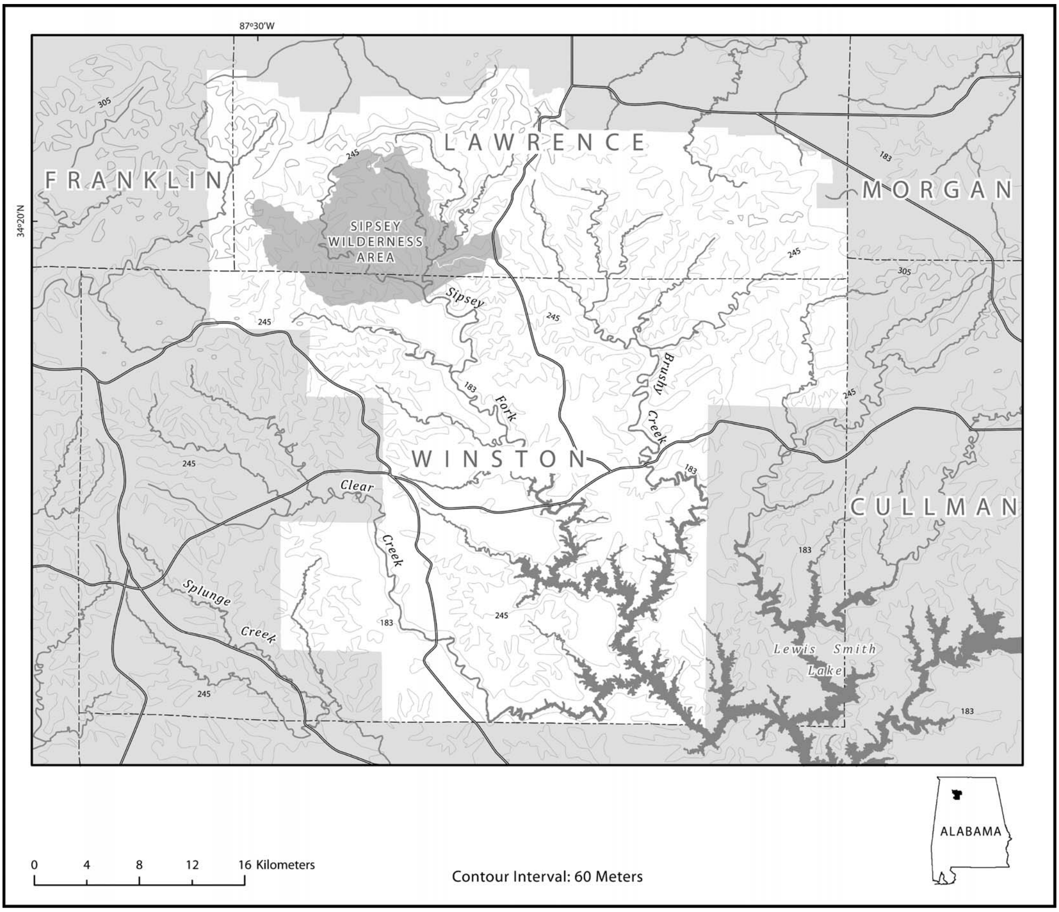

Figure 1. Map of the William B. Bankhead National Forest and the Sipsey Wilderness Area on the Cumberland Plateau in Alabama. White portion indicates the Bankhead National Forest.

posits that two or more disturbances in sequence may have cumulative or even multiplicative effects when compared to the isolated occurrences of the same events (e.g., Paine et al. 1998, Frelich 2002, Peterson and Leach 2008a). This sequence can be observed in the practice of salvage logging where forest stands impacted by a natural disturbance such as fire, insect outbreak, or windthrow are subsequently harvested. Such a quick series of disturbances is likely outside the historical disturbance regime and may facilitate a shift to an altered state (sensu Paine et al. 1998). Indeed, there is rising concern over the impact of salvage logging on the conservation of biodiversity and ecosystem resiliency (Foster and Orwig 2006, Lindenmayer and Noss 2006). Peterson and Leach (2008b) suggested that salvage events should be considered along a gradient, similar to the varying intensities of natural disturbances.

A recent tornado outbreak in northern Alabama accompanied by salvage logging provided the unique opportunity to test the effects of compounded disturbances on regeneration, specifically in the context of the *Quercus*-to-*Acer* transition. Our study focused on a site disturbed by the storm along the boundary of the Sipsey Wilderness Area within the William B. Bankhead National Forest (BNF) in Alabama (Figure 1). The USDA Forest Service contracted damaged areas to be salvaged. When disturbance extended into the Wilderness Area, salvage operations would progress up to the border without regard for ecological boundaries or stand delineations, leaving an array of disturbance combinations in close proximity. Thus, a unique opportunity arose to test the compounded disturbance hypothesis at a fine scale (i.e., within a single stand) and evaluate species responses, with particular attention on the *Quercus*-to-*Acer* transition.

The goal of this study was to examine the possible effects of compounded disturbance consisting of wind disturbance followed by salvage logging on stand development and successional pathways. We specifically compared neighborhoods within a single stand that represented a gradient of disturbance from undisturbed, wind-disturbed, and wind-disturbed followed by salvage logging to: (a) quantify species composition, size structure, and biodiversity of seedling and sapling layers, and (b) project canopy composition at crown closure.

MATERIALS AND METHODS

Study Area

The BNF is situated on the southern portion of the Cumberland Plateau, at the southern extent of the Appalachian Plateaus physiographic province (Fenneman 1938). The geology is primarily composed of the Pennsylvanian Pottsville formation and is characterized by thick-bedded to pebbly quartzose sandstone and contains variable levels of interstratified shale, siltstone, and thin coal seams (Szabo et al. 1988). The topography of this portion of the Cumberland Plateau is strongly dissected to such an extent that it does not truly resemble a plateau tableland (Smalley 1979). Elevation of the BNF spans from ca. 400 m amsl on the plateau surface to ca. 150 m amsl in the gorges. Regionally, soils are acidic, well drained, and shallow (USDA 1959).

The climate is classified as humid mesothermal (Thornthwaite 1948) and is characterized by short, mild winters and long, hot summers. The mean annual temperature is 16°C (January mean: 5°C, July mean: 26°C). The frost-free period is ca. 220 days and extends from late March to early November (Smalley 1979). The region has no distinct dry period as precipitation is distributed evenly throughout the year. Annual precipitation averages 1390 mm with monthly means of 135 and 113 mm for January and July, respectively (PRISM Climate Group 2013).

Plant communities on the Cumberland Plateau are influenced largely by topography and factors associated with soil-water availability (Hinkle 1989, Clatterbuck and Kauffman 2006). Cumberland Plateau forests are recognized for having high plant species richness and landscape-level diversity (Hinkle et al. 1993). Braun (1950) classified this region as a transition zone between the Mixed Mesophytic Forest to the north and the *Quercus-Pinus* Forest to the south. However, true mixed mesophytic communities occur only in shaded coves and riparian areas. Stands may contain taxa that typically dominate at both higher and lower latitudes, and environmental gradients are steep (Richards and Hart 2011, Parker and Hart 2014). Zhang et al. (1999) developed a classification scheme that included 14 different ecological communities on the Sipsey Wilderness Area portion within BNF. These community types ranged from xeric sites dominated by *Pinus virginiana* to mesic sites dominated by *Fagus grandifolia* and *Acer saccharum* to barren communities. *Quercus* was the most dominant genus in the Sipsey Wilderness Area and was a component of almost all community types (Zhang et al. 1999).

On 20 April 2011, an EF1 tornado embedded in a bow echo system impacted the BNF with sustained wind gusts between 130–145 kph (National Weather Service 2011). Storm damage was most severe in the tornado path and decreased in severity of disturbance with distance from the storm path. Following the event, the USDA Forest Service contracted salvage logging on accessible areas to recoup financial losses and reduce fuel loads. The sale consisted of 1,973 tonnes of *Pinus*, *Quercus*, and mixed hardwood sawtimber and pulpwood. Sawyers were allowed to cut downed and leaning trees and those with crown damage caused by the storm. Logs were cut with chainsaws and skidded to a landing near an existing road. Skidders had unrestricted access to logs and were equipped with rubber tractor tires and a grapple arm. All operations were completed by November 2011.

Field and Analytical Methods

Our study was focused in a single 49 ha stand. According to the USDA Forest Service Bankhead Ranger District inventory, the stand was dominated by *Quercus alba* and established in 1905. The sampled stand occurred in both the Sipsey Wilderness Area and in the larger BNF, and a portion of the stand across both management units was impacted by the storm. Thus, we were able to sample undisturbed, wind-disturbed, and wind-disturbed and salvage logged neighborhoods of the same stand. All sampling was conducted within a five ha area of a single stand and all analyzed neighborhoods were adjacent to each other. The neighborhoods that were sampled all occurred on the same land type according to Smalley's (1979) classification and based on Forest Service records had the same disturbance and management histories. All areas sampled were adjacent to the main storm path in what would be considered intermediate-scale disturbance (Cowden et al., 2014). In September and October of 2012 (two growing seasons after the wind disturbance), we established a total of 60 plots divided evenly among three disturbance classes: undisturbed (assumed to be predisturbance conditions using a space-for-time substitution), wind-disturbed, and salvaged (wind-disturbed + salvage logged). Plots were placed in a gridded pattern for systematic sampling of disturbed neighborhoods. In ArcMAP v 10 (ESRI, Redlands, California), we superimposed a 25 × 25 m grid oriented north over the three disturbance classes. A 40-m^2 circular vegetation plot was established at each intersection of the gridlines for a total of 20 plots per disturbance class. We required a minimum 25 m buffer around each plot from recreational trails, roads, and adjacent disturbance classes (the three neighborhoods sampled were all adjacent to each other) to prevent edge effects. Within each plot, all live woody stems regardless of size were identified to species and tallied by size class. Stems were classified into one of five size class bins: (a) <0.3 m ht, (b) 0.3–0.6 m ht, (c) >0.6–1.2 m ht, (d) >1.2 m ht and < 3.8 cm diameter at breast height (dbh), or (e) ≥ 3.8 cm dbh. The dbh was measured and recorded for all stems ≥3.8 cm. These size class breaks were used for predictive regeneration modeling. For other analyses individuals were grouped into three broader categories: seedling (<1.2 m ht), sapling (≥1.2 m ht and <5 cm dbh), or tree (≥5 cm dbh). Because of the low density of trees, only seedling and sapling data are reported here. However, trees were included in the predictive regeneration modeling.

We calculated seedling and sapling density (number of stems ha^{-1}), relative density (contribution to total stems), frequency (number of plots on which the species occurred), relative frequency (percent of plots on which the species occurred), and relative importance (sum of relative density and relative frequency) for seedlings and saplings of each disturbance class to examine general patterns. For each plot we calculated the following biodiversity measures: species richness (S), species evenness (J'), and the Shannon index (H'). We used Welch's one-way analysis of variance tests with Tukey honestly significant difference post-hoc tests ($P < 0.05$) to compare mean values of species richness, species evenness, and Shannon diversity per plot for the three disturbance classes.

To test for compositional differences, species were pooled into five functional groups (*A. rubrum*, *Quercus*, *Carya*, shrubs, and others; Table 1). We analyzed density data using two 3 × 5 factorial ANOVAs (one for seedlings and one for saplings), with one factor being the disturbance classes and one factor being the functional groups with Student-Newman-Keuls post-hoc tests to determine which variables were significantly different. All statistical tests were performed using SAS v. 9.3 (SAS Institute Inc., Cary, North Carolina).

Predictive Regeneration Model

We used the predictive regeneration model REGEN (Loftis 1989, 1990) to forecast composition and density of the three disturbance classes. The model is a multispecies, ranking-based expert system designed to be used following a stand-initiating disturbance at the point in time it enters the stem exclusion stage of development (Loftis 1989). The quantitative data reported by the model allows foresters to better prescribe regeneration and tending operations to achieve structural and compositional objectives. The model is dependent upon a REGEN knowledge base (RKB), which is a collection of rankings from one to eight for each species and size class based on qualitative species-specific abilities to capture growing space following a particular disturbance in the given biophysical setting. The most competitive stems are given a rank of one, and the least competitive stems are given a rank of eight. This allows for the prediction of up to six "winners" (i.e., those stems in the dominant or codominant canopy positions at the time of crown closure) per plot. If potential stump sprouts (stems ≥3.8 cm dbh) are captured in the plot, this number is reduced to four because of the increased growing space larger stems occupy. The plots were grouped according to disturbance class for analysis. Each RKB is developed by expert opinion and published literature and is also calibrated with field data for the unique region and general moisture

Table 1. All species included in each functional group used for comparisons and statistical tests on the Bankhead National Forest, Alabama

Acer rubrum
Acer rubrum L.
Quercus
Quercus alba L.
Quercus falcata Michx.
Quercus prinus L.
Quercus rubra L.
Quercus stellata Wangenh.
Quercus velutina Lam.
Carya
Carya alba L.
Carya glabra (Mill.) Sweet
Shrubs
Aralia spinosa L.
Crataegus spp.
Frangula caroliniana (Walter) A. Gray
Ilex opaca Aiton
Rhus glabra L.
Styrax grandifolius Aiton
Vaccinium arboreum Marsh.
Viburnum acerifolium L.
Others
Acer saccharum Marsh.
Asimina triloba (L.) Dunal
Betula lenta L.
Cornus florida L.
Diospyros virginiana L.
Fagus grandifolia Ehrh.
Fraxinus americana L.
Juniperus virginiana L.
Liquidambar styraciflua L.
Liriodendron tulipifera L.
Magnolia macrophylla Michx.
Nyssa sylvatica Marsh.
Oxydendrum arboreum L.
Pinus echinata L.
Pinus taeda L.
Pinus virginiana Mill.
Populus deltoides Marsh.
Prunus serotina Ehrh.
Sassafras albidum (Nutt.) Nees
Ulmus alata Michx.
Ulmus rubra Muhl.

regime. For example, Vickers et al. (2011) created preliminary RKBs for xeric, subxeric, submesic, and mesic sites on the Allegheny Plateau and the Ridge and Valley Physiographic provinces. The RKB used for this study was developed for the escarpment region of the Cumberland Plateau in eastern Tennessee and was adapted for this study. The REGEN model requires data be surveyed within a 40 m^2 fixed radius plot and advance reproduction classified into one of the aforementioned size classes. Probabilistic establishment factors are used for new seedlings, potential stump sprouts, and root suckers.

RESULTS AND DISCUSSION

Influences on Regeneration and Diversity

Seedling (all woody stems <1.2 m ht) density of the undisturbed, wind-disturbed, and wind-disturbed and salvaged disturbance classes was 17,488, 13,788, and 15,638 stems ha^{-1}, respectively (Table 2). *Quercus prinus*, *Q. velutina*, *Q. rubra*, and *Q. alba* combined represented 54% of all seedlings on undisturbed plots, 41% on wind-disturbed plots, and 28% on salvaged plots. All four of these *Quercus* species occurred on at least 60% of the plots in all disturbance classes. *Acer rubrum* exhibited the highest seedling density of any species on the salvaged plots and was the fifth and tied as the second most abundant species in the seedling layer on undisturbed and wind-disturbed plots, respectively.

Sapling (all woody stems $\geq$1.2 m ht and <5 cm dbh) density of undisturbed, wind-disturbed, and salvaged classes was 2,588, 4,113, and 2,275 stems ha^{-1}, respectively (Table 3). Sapling density in wind-disturbed and unsalvaged areas was 82% greater than density in salvaged areas. Our findings indicate salvage operations were responsible for sapling mortality, which was also observed by Cannon and Brewer (2013) in Mississippi. *Quercus prinus*, *Q. velutina*, *Q. rubra*, and *Q. alba* collectively represented just 9% of saplings on undisturbed plots, 18% on wind-disturbed plots, and 9% on salvaged plots (Table 3). In addition, with the exception of *Q. velutina* in the wind disturbance class, no *Quercus* species saplings occurred on 50% of the plots in any disturbance category. *Acer rubrum* was overwhelmingly the most abundant sapling across all disturbance classes and this species occurred on at least 80% of all plots in each disturbance category. Our results exhibited the *Quercus*-to-*Acer* transition that has been noted in *Quercus*-dominated stands throughout the Central Hardwood Forest of the eastern US (Nowacki and Abrams 2008, Fei and Steiner 2009, McEwan et al. 2011). Although variability exists, most *Quercus* species are only moderately tolerant of shade and regeneration is inhibited in stands with an abundance of shade-tolerant individuals in the sapling layer (Lorimer et al. 1994). Thus, we postulate the abundance of *A. rubrum* in the sapling layer inhibited the recruitment of *Quercus* seedlings to larger size classes. Although *Quercus* seed-

Table 2. Seedling (woody stems <1.2 m ht) density (number of stems), relative density (percent of total stems), frequency (number of plots on which species occurred), relative frequency (percent of plots on which species occurred) and relative importance (sum of relative density and relative frequency) for undisturbed (UND), wind-disturbed (WIND), and wind-disturbed and salvaged (SAL) classes on the Bankhead National Forest, Alabama

	Density (stems ha^{-1})			Relative Density			Frequency			Relative Frequency			Relative Importance		
Species	**UND**	**WIND**	**SAL**	**UND**	**WIND**	**SAL**	**UND**	**WIND**	**SAL**	**UND**	**WIND**	**SAL**	**UND**	**WIND**	**SAL**
Acer rubrum	1,888	1,825	3,075	10.8	13.2	19.7	19	19	20	95.0	95.0	100.0	105.8	108.2	119.7
Acer saccharum	200	0	38	1.1	0.0	0.2	4	0	2	20.0	0.0	10.0	21.1	0.0	10.2
Asimina triloba	38	38	75	0.2	0.3	0.5	3	2	2	15.0	10.0	10.0	15.2	10.3	10.5
Betula lenta	13	38	50	0.1	0.3	0.3	1	2	3	5.0	10.0	15.0	5.1	10.3	15.3
Carya spp.[1]	625	1,038	875	3.6	7.5	5.6	17	18	17	85.0	90.0	85.0	88.6	97.5	90.6
Cornus florida	13	25	38	0.1	0.2	0.2	1	2	2	5.0	10.0	10.0	5.1	10.2	10.2
Crataegus spp.	13	0	63	0.1	0.0	0.4	1	0	4	5.0	0.0	20.0	5.1	0.0	20.4
Diospyros virginiana	75	363	1,113	0.4	2.6	7.1	3	17	18	15.0	85.0	90.0	15.4	87.6	97.1
Frangula caroliniana	575	1,138	88	3.3	8.3	0.6	8	12	4	40.0	60.0	20.0	43.3	68.3	20.6
Fraxinus americana	0	88	25	0.0	0.6	0.2	0	5	1	0.0	25.0	5.0	0.0	25.6	5.2
Liriodendron tulipifera	13	325	388	0.1	2.4	2.5	1	8	9	5.0	40.0	45.0	5.1	42.4	47.5
Nyssa sylvatica	138	213	400	0.8	1.5	2.6	7	9	11	35.0	45.0	55.0	35.8	46.5	57.6
Others[2]	38	75	63	0.2	0.5	0.4	3	4	4	15.0	20.0	20.0	15.2	20.5	20.4
Pinus taeda	0	50	0	0.0	0.4	0.0	0	3	0	0.0	15.0	0.0	0.0	15.4	0.0
Prunus serotina	288	188	188	1.6	1.4	1.2	10	11	8	50.0	55.0	40.0	51.6	56.4	41.2
Quercus alba	2,500	2,938	1,538	14.3	21.3	9.8	17	20	13	85.0	100.0	65.0	99.3	121.3	74.8
Quercus falcata	25	25	88	0.1	0.2	0.6	2	2	1	10.0	10.0	5.0	10.1	10.2	5.6
Quercus prinus	3,588	1,338	1,825	20.5	9.7	11.7	18	15	15	90.0	75.0	75.0	110.5	84.7	86.7
Quercus rubra	1,250	425	488	7.1	3.1	3.1	19	12	13	95.0	60.0	65.0	102.1	63.1	68.1
Quercus velutina	2,038	963	563	11.7	7.0	3.6	19	19	14	95.0	95.0	70.0	106.7	102.0	73.6
Sassafras albidum	600	38	688	3.4	0.3	4.4	5	2	10	25.0	10.0	50.0	28.4	10.3	54.4
Styrax glandifolius	113	38	2,438	0.6	0.3	15.6	2	2	12	10.0	10.0	60.0	10.6	10.3	75.6
Vaccinium arboreum	1,338	800	563	7.6	5.8	3.6	17	17	8	85.0	85.0	40.0	92.6	90.8	43.6
Viburnum acerifolium	2,125	1,825	975	12.2	13.2	6.2	15	14	8	75.0	70.0	40.0	87.2	83.2	46.2
Total	**17,488**	**13,788**	**15,638**	**100**	**100**	**100**	–	–	–	–	–	–	–	–	–

[1]*Carya* spp. includes *Carya alba* and *Carya glabra*.

[2]Others = All three RIVs were <10.0. Includes *Aralia spinosa*, *Fagus grandifolia*, *Ilex opaca*, *Juniperus virginiana*, *Liquidambar styraciflua*, *Magnolia macrophylla*, *Oxydendrum arboretum*, *Populus deltoides*, *Quercus stellata*, and *Ulmus alata*.

lings are often abundant, their presence is typically ephemeral as they are subsequently outcompeted by *A. rubrum* (i.e., they cannot pass through the *Quercus* bottleneck; Arthur et al. 2012).

Mean species richness, Shannon diversity, and evenness per plot did not significantly differ across the three disturbance classes (Table 4), which is consistent with some other studies (e.g., Peterson and Leach 2008a, Lang et al. 2009,

Table 3. Sapling (≥1.2 m ht and <5 cm dbh) density (number of stems), relative density (percent of total stems), frequency (number of plots on which species occurred), relative frequency (percent of plots on which species occurred) and relative importance (sum of relative density and relative frequency) for undisturbed (UND), wind-disturbed (WIND), and wind-disturbed and salvaged (SAL) classes on the Bankhead National Forest, Alabama

	Density (stems ha^{-1})			Relative Density			Frequency			Relative Frequency			Relative Importance		
Species	**UND**	**WIND**	**SAL**	**UND**	**WIND**	**SAL**	**UND**	**WIND**	**SAL**	**UND**	**WIND**	**SAL**	**UND**	**WIND**	**SAL**
Acer rubrum	1,000	1,350	925	38.6	32.8	40.7	18	16	17	90.0	80.0	85.0	128.6	112.8	125.7
Acer saccharum	25	0	13	1.0	0.0	0.5	2	0	1	10.0	0.0	5.0	11.0	0.0	5.5
Asimina triloba	50	0	0	1.9	0.0	0.0	4	0	0	20.0	0.0	0.0	21.9	0.0	0.0
Betula lenta	13	13	25	0.5	0.3	1.1	1	1	2	5.0	5.0	10.0	5.5	5.3	11.1
Carya spp.[1]	213	413	75	8.2	10.0	3.3	12	15	7	60.0	75.0	35.0	68.2	85.0	38.3
Cornus florida	0	50	0	0.0	1.2	0.0	0	2	0	0.0	10.0	0.0	0.0	11.2	0.0
Diospyros virginiana	0	150	150	0.0	3.6	6.6	0	6	7	0.0	30.0	35.0	0.0	33.6	41.6
Fagus grandifolia	63	0	0	2.4	0.0	0.0	2	0	0	10.0	0.0	0.0	12.4	0.0	0.0
Frangula caroliniana	175	688	25	6.8	16.7	1.1	5	12	2	25.0	60.0	10.0	31.8	76.7	11.1
Fraxinus americana	0	25	25	0.0	0.6	1.1	0	2	2	0.0	10.0	10.0	0.0	10.6	11.1
Liriodendron tulipifera	13	38	0	0.5	0.9	0.0	1	2	0	5.0	10.0	0.0	5.5	10.9	0.0
Nyssa sylvatica	113	13	63	4.3	0.3	2.7	5	1	3	25.0	5.0	15.0	29.3	5.3	17.7
Others[2]	13	138	0	0.5	3.3	0.0	1	8	0	5.0	40.0	0.0	5.5	43.3	0.0
Prunus serotina	75	250	75	2.9	6.1	3.3	5	14	5	25.0	70.0	25.0	27.9	76.1	28.3
Quercus alba	38	163	0	1.4	4.0	0.0	2	9	0	10.0	45.0	0.0	11.4	49.0	0.0
Quercus prinus	88	213	75	3.4	5.2	3.3	4	7	4	20.0	35.0	20.0	23.4	40.2	23.3
Quercus rubra	63	75	75	2.4	1.8	3.3	5	3	4	25.0	15.0	20.0	27.4	16.8	23.3
Quercus velutina	50	288	50	1.9	7.0	2.2	4	11	3	20.0	55.0	15.0	21.9	62.0	17.2
Sassafras albidum	50	38	25	1.9	0.9	1.1	3	1	1	15.0	5.0	5.0	16.9	5.9	6.1
Styrax glandifolius	225	75	613	8.7	1.8	26.9	2	2	7	10.0	10.0	35.0	18.7	11.8	61.9
Vaccinium arboreum	250	75	13	9.7	1.8	0.5	10	4	1	50.0	20.0	5.0	59.7	21.8	5.5
Viburnum acerifolium	75	63	50	2.9	1.5	2.2	3	3	1	15.0	15.0	5.0	17.9	16.5	7.2
Total	**2,588**	**4,113**	**2,275**	**100**	**100**	**100**	–	–	–	–	–	–	–	–	–

[1]*Carya* spp. includes *Carya alba* and *Carya glabra*.

[2]Others = All three RIVs <10.0. Includes *Aralia spinosa*, *Ilex opaca*, *Juniperus virginiana*, *Magnolia macrophylla*, *Oxydendrum arboretum*, *Quercus falcata*, *Quercus stellata*, *Rhus glabra*, and *Ulmus rubra*.

Table 4. Mean species richness, diversity, and evenness per plot ± standard error for woody plants according to disturbance class in the Bankhead National Forest, Alabama. Means in rows followed by same letter are not significantly different at $p < 0.05$

	Undisturbed	**Wind**	**Wind + Salvage**
Species richness (*S*)	11.45 ± 0.63 a	12.90 ± 0.50 a	10.90 ± 0.60 a
Shannon-Wiener index (*H'*)	1.89 ± 0.02 a	2.08 ± 0.02 a	1.85 ± 0.03 a
Species evenness (*J'*)	0.82 ± 0.06 a	0.82 ± 0.06 a	0.78 ± 0.09 a

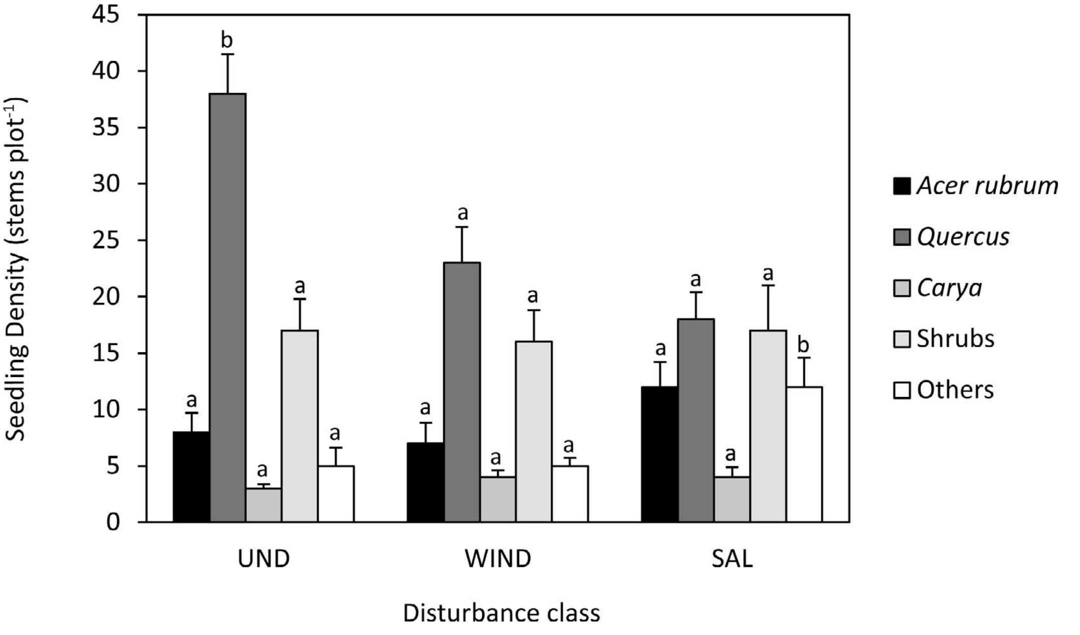

Figure 2. Mean densities with standard errors for seedlings (<1.2 m ht) by functional group in undisturbed (UND), wind-disturbed (WIND), and wind-disturbance and salvaged (SAL) classes. Bars with different lowercase letters within functional groups represent significant differences ($p < 0.05$) among disturbance classes.

D'Amato et al. 2011). We documented nine species that were unique to one disturbance category: *Aralia spinosa*, *Magnolia macrophylla*, *Oxydendrum arboreum*, *Pinus taeda*, and *Rhus glabra* in wind-disturbed plots; *Liquidambar styraciflua*, *Populus deltoides*, and *Ulmus alata* in salvaged; and *Ulmus rubra* in undisturbed plots. Of these nine species, only *O. arboreum* and *P. taeda* occurred in more than one plot. Despite the presence or increase of shade-intolerant species such as *P. taeda*, *L. styraciflua*, and *L. tulipifera* in disturbed neighborhoods relative to undisturbed areas, two growing seasons after the disturbances alpha-level diversity (i.e., diversity at the stand scale) was unchanged.

We found no significant differences in the density of seedlings among the three disturbance classes (ANOVA: $df = 2$, $F = 2.19$, $p = 0.1141$), but we did note significant differences in the mean density of seedlings among functional groups (ANOVA: $df = 4$, $F = 43.96$, $p < 0.0001$; Figure 2). Our results also revealed a significant interaction between disturbance classes and functional groups for the seedling layer (ANOVA: $df = 8$, $F = 5.28$, $p < 0.0001$). The mean density of saplings on wind-disturbed plots was significantly higher than sapling density on undisturbed and salvaged plots (ANOVA: $df = 2$, $F = 7.68$, $p = 0.0006$; Figure 3). We also found significant differences in the mean density of saplings by functional group (ANOVA: $df = 4$, $F = 14.54$, $p < 0.0001$). Our results did not reveal significant interactions between disturbance class and functional group for the sapling layer (ANOVA: $df = 8$, $F = 0.28$, $p = 0.9708$).

The density of *Quercus* seedlings decreased along the disturbance intensity gradient (from undisturbed, to wind-disturbed, to wind-disturbed and salvaged). In contrast, seedling densities of *A. rubrum* and the others groups were similar between undisturbed and wind-disturbed plots, but increased with disturbance intensity (from wind-disturbed to wind-disturbed and salvaged). *Quercus* seedlings were more abundant in the undisturbed plots compared to the disturbed plots, but *Quercus* saplings were most abundant in wind-disturbed plots. We hypothesized this pattern may have resulted from recruitment of seedling-sized *Quercus* stems to the sapling size class following overstory removal. As previously stated, *Quercus* reproduction is only moderately tolerant of shade and seedlings are typically considered

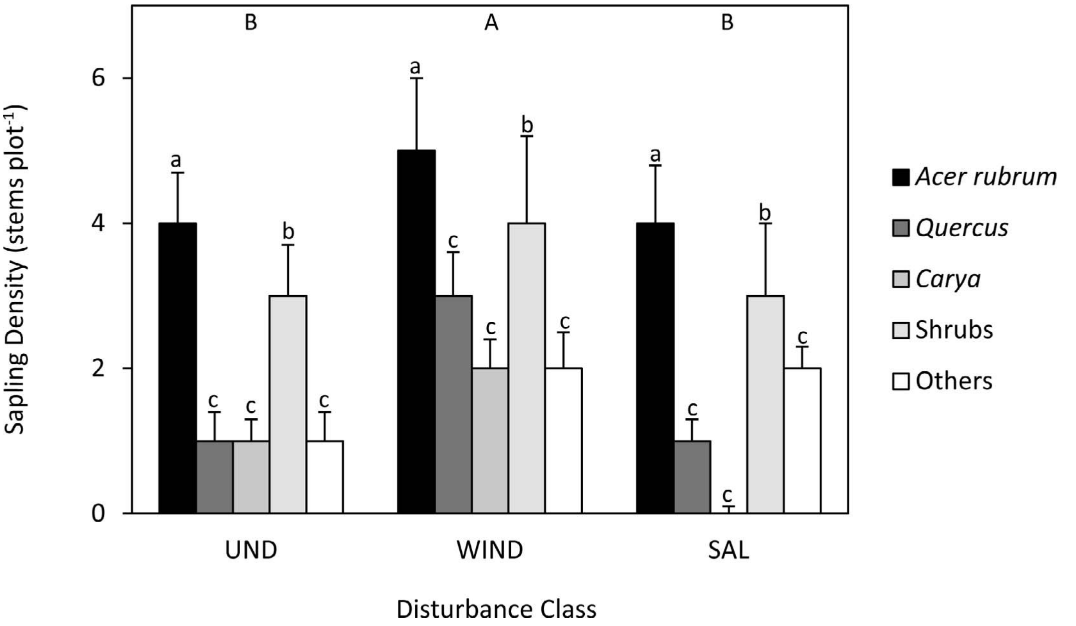

Figure 3. Mean densities with standard errors for saplings (≥1.2 m ht and <5 cm dbh) by functional group in undisturbed (UND), wind-disturbed (WIND), and wind-disturbed and salvaged (SAL) classes. Functional groups with different lowercase letters are significantly different ($p < 0.05$) from other functional groups and different capital letters above disturbance classes signify significant differences among disturbance classes.

ephemeral in the absence of canopy disturbance. Suppressed and small *Quercus* stems have been shown to rapidly respond to changes in the light regime (Nowacki and Abrams 1997, Rentch et al. 2003, Buchanan and Hart 2012). We speculate that *Quercus* sapling density in the salvaged areas was low compared to the unsalvaged areas because of damage caused by the harvesting operation. Schweitzer and Dey (2013) did not find differences in mortality rates of *Quercus* seedlings and saplings across variable intensities of logging equipment traffic. However, differences in mortality of small *Quercus* may be apparent between logged and unlogged areas.

Density of *Acer rubrum* seedlings and saplings was similar for each disturbance category. Unlike *Quercus* seedlings, small *A. rubrum* do not require canopy disturbance within the first decade of life for establishment and are thus not ephemeral in absence of disturbance. Seedling density of *A. rubrum* was comparatively low and significantly lower than *Quercus* in both wind-disturbed and undisturbed plots. However, *A. rubrum* seedling frequency was the highest of all species, as it was found on at least 95% of all plots across all three disturbance classes. Likewise, the frequency of *A. rubrum* saplings was the highest of any species as it occurred on 80%, 85%, and 90% of wind-disturbed, salvaged, and undisturbed plots, respectively. Across seedling and sapling size classes and all disturbance classes, the *Carya* group was consistently the least represented. Interestingly, the shrub category was the second most abundant group in the sapling layer across all disturbance categories.

The salvaged plots had 70% and 81% fewer *Quercus* and *Carya* saplings relative to the wind-disturbed and unsalvaged plots, respectively. In contrast, *A. rubrum* sapling density was only 31% lower on salvaged vs. wind-disturbed and unsalvaged classes. Stringer (2006) measured survival of advanced reproduction after a regeneration harvest in a *Quercus* stand on the Cumberland Plateau in central Kentucky. Harvesting techniques were almost identical to those conducted in this study for the salvage operations. *Quercus* reproduction had a 67% chance of survival after logging operations, whereas *Acer* species averaged 80% survival. Stringer (2006) concluded that *Quercus* seedlings incur substantially greater reductions in

Table 5. Projected density and relative density of undisturbed (UND), wind-disturbed (WIND), and wind-disturbed and salvaged (SAL) classes at the onset of the stem exclusion stage of development using the REGEN predictive model

	Density (stems ha^{-1})			Relative Density (%)		
Species	**UND**	**WIND**	**SAL**	**UND**	**WIND**	**SAL**
Acer rubrum	579	403	406	56.7	36.9	32.5
Quercus prinus	89	94	66	8.7	8.6	5.3
Styrax grandifolius	80	5	198	7.8	0.5	15.8
Nyssa sylvatica	47	4	21	4.6	0.4	1.7
Prunus serotina	34	90	46	3. 4	8.3	3.7
Quercus velutina	32	67	25	3.1	6.1	2.0
Quercus rubra	27	26	53	2.7	2.3	4.2
Liriodendron tulipifera	26	214	186	2.5	19.6	14.9
Sassafras albidum	23	0	6	2.2	0.0	0.5
Pinus taeda	20	76	116	1.9	6.9	9.3
Betula lenta	19	36	88	1.9	3.3	7.1
Carya glabra	14	17	6	1.4	1.5	0.5
Acer saccharum	9	–	17	0.9	–	1.3
Quercus alba	9	2	0	0.8	0.2	0.0
Fagus grandifolia	6	6	–	0.6	0.6	
Carya alba	5	1	–	0.5	0.1	–
Oxydendron arboreum	1	2	–	0.1	0.2	–
Quercus stellata	1	4	–	0.1	0.4	–
Frangula caroliniana	0	–	–	0.0	–	–
Cornus florida	0	–	–	0.0	–	–
Fraxinus americana	–	32	15	–	3.0	1.2
Diospyros virginiana	–	1	1	–	0.1	0.1
Juniperus virginiana	–	12	–	–	1.1	–
Quercus falcata	–	0	–	–	0.0	–
Groups						
Acer rubrum	579	403	406	56.7	36.9	32.5
Quercus	158	193	144	15.5	17.6	11.5
Carya	19	17	6	1.9	1.6	0.5
Shrubs	80	5	198	7.8	0.5	15.8
Others	185	475	497	18.1	43.4	39.7
Total	**1,021**	**1,093**	**1,251**	**100.0**	**100.0**	**100.0**

density than co-occurring species. Perhaps this pattern was related to stem flexibility; *A. rubrum* may be more able to bend without snapping while *Quercus* may be likely to break.

In each of the disturbance classes, *Quercus* advanced reproduction was found to be underrepresented to dominate the future stand. *Quercus* is dependent upon stems established in the regeneration layer to comprise a component of the future stand after stand-initiating disturbance and is typically not successful "seeding in" (i.e., regenerating from seed and establishing dominance following disturbance event) (Dey 2002). We note that our study was conducted within a single stand, and our disturbance classes were not replicated in other stands. Thus, seemingly small differences in the predisturbance conditions of these adjacent neighborhoods of the same stand may have influenced our results. In addition, our sampling was conducted just two growing seasons after the wind disturbance event. Thus, repeat sampling might reveal patterns that emerge as the stands develop.

Predicted Composition by REGEN Model

Acer rubrum was predicted to be the most abundant species in the undisturbed class, estimated to be 579 stems ha^{-1} and represent 57% of all stems at crown closure (Table 5). *Quercus prinus*, *S. grandifolius*, and *Nyssa sylvatica* were predicted as the next most prevalent species with 89, 80, and 47 stems ha^{-1}, respectively, and relative densities of 9%, 8%, and 5%, respectively. The model predicted *Quercus* stem density at 158 stems ha^{-1}, which would represent 16% of all stems.

In the wind disturbance class, *A. rubrum* was predicted to be the most abundant species with

403 trees ha^{-1} and a relative density of 37%. The next most abundant species were projected to be *Liriodendron tulipifera*, *Q. prinus*, and *Prunus serotina* with densities of 214, 94, and 90 trees ha^{-1}, respectively, and relative densities of 20%, 9%, and 8%, respectively. At the functional group level, "others" was predicted to be the most abundant (475 stems ha^{-1}), but the model projected this category would largely be comprised of *L. tulipifera*. The model predicted *Quercus* density would be 193 trees ha^{-1}, which would be less than half the density of *A. rubrum*. In the salvaged class, *A. rubrum* was predicted to be the most abundant species with 406 trees ha^{-1} and a relative density of 37%. The next most abundant species predicted were *S. grandifolius*, *L. tulipifera*, and *P. taeda* with densities of 198, 186, and 116 trees ha^{-1} respectively and relative densities of 16%, 15%, and 9% respectively.

At the onset of the stem exclusion stage of development, the model predicted that stem density would increase along the disturbance gradient from undisturbed, wind damaged, to wind damaged and salvaged disturbance classes. Across all disturbance categories, *Acer rubrum* was predicted to be most abundant species at the time of stem exclusion. The *A. rubrum* group was also predicted to be the most abundant compared to the other taxonomic groupings used in our study. These results beg the question: can *A. rubrum* attain canopy dominance in this region and if so what circumstances or sequences of events lead to this pattern? In a gradient analysis study of the Sipsey Wilderness Area of the BNF, Zhang et al. (1999) noted 14 distinct ecological communities, including an *A. rubrum* community type. In this community type, *A. rubrum* represented 15% of the basal area, but the species represented 36% and 45% of the basal area in the *F. grandifolia*/*A. saccharum* and *Tsuga canadensis* L. community types, respectively (Zhang et al. 1999). Thus, on some sites of the BNF *A. rubrum* must be able to represent a large component of canopy dominant trees. Hart et al. (2012) analyzed the canopy accession strategy of *A. rubrum* on the tablelands of the Cumberland Plateau in Tennessee and found that *A. rubrum* was a gap opportunist, but that stems could still attain canopy positions after being suppressed for long periods. They also speculated that *A. rubrum* would become a major component of the canopy stratum for at least portions of the study area. We are uncertain the extent to which *A. rubrum* can dominate the canopy of sites that are currently dominated by upland *Quercus* species.

The model predicted *Quercus* and *Carya* densities at stem exclusion in the salvaged class to be 33% and 200% lower than in the wind-disturbed and unsalvaged class, respectively. *Quercus prinus* was predicted to be the most abundant species of its genus in each disturbance class. However, in the salvaged category it was ranked sixth in relative density by the model, whereas it was ranked second and third in undisturbed and wind-disturbed categories, respectively. No *Quercus* species, except *Q. rubra*, was predicted to be higher in density or relative density in salvaged vs. unsalvaged classes. In contrast, "shrubs" was predicted to be 3,628% greater in the salvaged category (198 stems ha^{-1}) compared to the wind-disturbed category (5 stems ha^{-1}) at the time of stem exclusion. Within the "shrubs" group, *S. grandifolius* in particular was predicted to proliferate within both undisturbed and salvaged areas. However, it should be noted that the REGEN model predicts density and composition when the stand enters the stem exclusion phase of development. Since this species cannot ascend to the height of a mature canopy (maximum height = 6 m; USDA Plant Database 2014), we hypothesized that as stem exclusion progresses the salvaged class would lose the majority of *S. grandifolius* presence and would have an *Acer rubrum*/*Liriodendron tulipifera*/*Pinus taeda* composition before entering the understory reinitiation phase.

SUMMARY Our results indicate that wind disturbance in an upland *Quercus* stand that supports a high density of shade-tolerant stems in the understory, accelerates succession toward dominance by shade-tolerant taxa (i.e., disturbance-mediated accelerated succession). Based on our findings, we posit that salvage operations following wind disturbance in such stands may amplify the replacement process of *Quercus* with shade-tolerant species, notably *A. rubrum*.

The salvage operation appeared to reduce the density of *Quercus* saplings without reducing *A. rubrum* competition. However, even in the wind-disturbed and unsalvaged disturbance class, the class in which *Quercus* density at stem exclusion was predicted to be the highest, *A. rubrum* was still predicted to have more than twice the density of all *Quercus* species combined. *Quercus* stocking in both disturbance categories was insufficient to promote *Quercus* to its predisturbance prominence in the overstory. Thus, although the salvage operation appeared to hasten the *Quercus*-to-*Acer* transition, wind-disturbed and unsalvaged neighborhoods still lacked sufficient *Quercus* advanced reproduction and were projected to support a high density of *A. rubrum* at crown closure.

Our study indicated that regardless of salvage logging, passive management is not a viable option for landowners desiring to maintain *Quercus* dominance in wind-disturbed stands that have a high density of shade-tolerant saplings, especially *A. rubrum*. In stands with abundant *A. rubrum* in the understory, a lack of competition control such as fire or herbicide application following catastrophic or intermediate-scale disturbance may cause a marked shift towards *A. rubrum* dominance (Loftis 1990, Schweitzer and Dey 2011, Hutchinson et al. 2012, Brose et al. 2013). Although such natural disturbances are stochastic, managers may be best advised to have a plan prepared for such events and should realize that control of *A. rubrum* may become more problematic following a salvage operation.

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