Forest Ecology and Management 400 (2017) 110–122

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Effects of intermediate-severity disturbance on composition and structure in mixed *Pinus*-hardwood stands

Benjamin W. Trammell [a], Justin L. Hart [a,*], Callie J. Schweitzer [b], Daniel C. Dey [c], Michael K. Steinberg [a]

[a] Department of Geography, University of Alabama, Tuscaloosa, AL 35487, USA
[b] Southern Research Station, USDA Forest Service, Huntsville, AL 35801, USA
[c] Northern Research Station, USDA Forest Service, Columbia, MO 65211, USA

ARTICLE INFO

Article history:
Received 10 April 2017
Received in revised form 26 May 2017
Accepted 30 May 2017

Keywords:
Pinus (pine)
Quercus (oak)
Stand structure
Succession
Wind disturbance

ABSTRACT

Increasingly, forest managers intend to create or maintain mixed *Pinus*-hardwood stands. This stand assemblage may be driven by a variety of objectives but is often motivated by the desire to enhance native forest diversity and promote resilience to perturbations. Documenting the effects of natural disturbances on species composition and stand structure, and thus successional and developmental pathways, in stands with these mixtures is essential to achieve these goals. The specific objectives of this study were to quantify and compare the impacts of an intermediate-severity canopy disturbance on woody species composition, canopy structure, understory light regimes, and species diversity in mixed *Pinus* (*Pinus taeda* and *Pinus virginiana*)-hardwood stands on the Cumberland Plateau in Alabama. The natural intermediate-severity disturbance disproportionately removed large *Pinus* stems, promoted hardwood dominance, and effectively accelerated succession. The resultant stand structure did not resemble one of the widely recognized stages of stand development and was best characterized by the mixed-stage of development. The canopy disturbance did not significantly alter canopy-layer species diversity, but seedling- and sapling-layer diversity was significantly greater in disturbed neighborhoods. Results from this study may be used as guidelines by managers of mixed *Pinus*-hardwood systems. To maintain a *Pinus* component in stands that are succeeding to hardwood dominance, canopy disturbance alone is insufficient and must be planned in conjunction with competition reduction measures in the regeneration layer, such as fire or herbicide application. Conversely, if managers wish to promote a hardwood component in pure or near pure *Pinus* stands, creation of variably sized canopy openings throughout the stand may recruit hardwood reproduction to larger size classes, as the intermediate-severity disturbance documented here accelerated succession toward hardwood dominance.

1. Introduction

Forest disturbances, events to which all forest ecosystems are subject, disrupt the biophysical environment and influence developmental and successional processes (White and Pickett, 1985; Foster et al., 1998). Forest disturbances are typically classified based on severity, spatial extent, and frequency and range from small, frequent, single-tree gaps to large, infrequent, stand replacing events (Oliver and Larson, 1996). Intermediate-severity disturbances (ISD) occur along the gradient between the two endpoints (Cowden et al., 2014). Natural agents that may result in an ISD include strong wind events (e.g., tornadoes, downbursts from convective storms, and hurricanes), mixed-severity fires, ice storms, insect outbreaks, and diseases (Oliver and Larson, 1996; Peterson, 2000; Nagel and Diaci, 2006; Hart et al., 2008). Although disturbance agents and the effects of discrete ISD events vary widely, all ISDs typically alter the availability of light in the understory, which is regarded as the most common limiting abiotic factor in closed canopy forests (Canham and Loucks, 1984; Oliver and Larson, 1996; Hanson and Lorimer, 2007; Grayson et al. 2012). Intermediate-severity disturbances disrupt larger areas than gap-scale events and have a shorter return interval than the lifespan of most canopy trees (Canham and Loucks, 1984; Lorimer, 2001; Seymour et al., 2002; Hanson and Lorimer, 2007; Cowden et al., 2014; White et al. 2015), yet surprisingly little quantitative information is available on their influence in forest ecosystems.

The mixed *Pinus*-hardwood forest type spans millions of hectares throughout the eastern USA (Cooper, 1989; Smith and Darr, 2004). In the southeastern USA, many contemporary mixed *Pinus*-hardwood stands established as a result of land clearing for agriculture and subsequent abandonment (Cooper, 1989; Keeley

* Corresponding author.
E-mail address: hart013@ua.edu (J.L. Hart).

http://dx.doi.org/10.1016/j.foreco.2017.05.055
0378-1127/

and Zedler, 1998). Patterns of natural succession in such mixed *Pinus*-hardwood stands have been established (Peet and Christensen, 1980; Cooper, 1989; Shelton and Cain, 1999). The open, and sometimes low-fertility, conditions in old fields favor the establishment of early-seral *Pinus* stems. In the absence of fire, more shade-tolerant hardwoods typically establish in these stands, and an abundance of hardwood advanced reproduction in the understory inhibits *Pinus* regeneration. Without active management or relatively broad-scale natural disturbance, the *Pinus* component of these stands will diminish and the dominance of hardwood species will increase (Cooper, 1989; Guyette et al., 2007; Hart et al. 2012a; Weber et al., 2014).

Managers in the Central Hardwood Forest region are increasingly tasked with maintaining or creating *Pinus*-hardwood mixtures to meet a range of objectives including increased biodiversity, achieving desired fuel loads, enhanced resiliency to perturbations, commodity production, and restoration goals (Hart et al., 2012a; Clabo and Clatterbuck, 2015). Mixed *Pinus*-hardwood stands may be more structurally heterogeneous than pure *Pinus* or pure hardwood stands. As mixed stands contain tree species that represent a range of life history characteristics and growth forms (e.g. deciduous v. evergreen foliage), these stands may promote biological diversity by providing a comparatively wide range of habitat niche space for other organisms. For example, some wildlife species such as *Picoides borealis* Vieillot (red-cockaded woodpecker), *Sitta pusilla* Latham (brown-headed nuthatch), and *Setophaga pinus* Wilson (pine warbler) are associated with mature *Pinus* trees (Johnston and Odum, 1956; Dickson, 1982; Buckner, 1982; Owen, 1984). The acidic and highly flammable *Pinus* litter also provides a pathway for change in these systems. *Pinus* litter is considered highly flammable relative to some hardwood litter and promotes the spread of fire (Keeley and Zedler, 1998; Kane et al., 2008; Ellair and Platt, 2013). The *Pinus*-hardwood mixture may also promote resiliency to future disturbances, as well as provide options for uncertain future timber markets (Cooper, 1989; Clabo and Clatterbuck, 2015). Quantitative descriptions of the effects of natural and anthropogenic intermediate-severity disturbances in mixed *Pinus*-hardwood stands are needed to provide data necessary to actively manage in accord with natural processes, and develop silvicultural systems designed to create or maintain mixed *Pinus*-hardwood systems.

This study addressed a void in our understanding of the effects of intermediate-severity wind disturbance on species composition and succession, stand structure and development, and sub-canopy light regimes in mixed *Pinus*-hardwood stands. Additionally, this study serves as a reference point for natural disturbance-based management in this forest type. The specific objectives of this study were to quantify and compare effects of an ISD on woody species composition, stand structure, understory light regimes, and species diversity in mixed *Pinus*-hardwood stands. Our results provide quantitative information on the effects of natural intermediate-severity disturbances, which have been vastly understudied relative to catastrophic and gap-scale disturbances. This information may be used to develop silvicultural systems designed to retain a *Pinus* component in stands that are transitioning to hardwood dominance or conversely, to accelerate succession to hardwood dominance to achieve mixed *Pinus*-hardwood assemblages in pure or nearly pure *Pinus* stands.

2. Study area and methods

2.1. Study area

Our study was conducted on the William B. Bankhead National Forest in northern Alabama. The Bankhead National Forest occurs on the Cumberland Plateau section of the Appalachian Plateaus physiographic province (Fenneman, 1938). The topography of the region is distinguished by its locally high relief with narrow ridges, steep slopes, and deep valleys. The area is so strongly dissected that it does not resemble a true plateau (Smalley, 1979). The underlying geology of the region is Pennsylvanian quartzose sandstone containing interstratified layers of limestone, shale, siltstone, and discontinuous anthracite and bituminous coal (Szabo et al., 1988). Soils in the region are generally shallow, acidic and well-drained (USDA SCS, 1959). The regional climate is classified as humid mesothermal, characterized by long, hot summers and short, mild winters (Thornthwaite, 1948). The mean annual temperature is 16 °C, with average temperatures in January and July of 5 °C and 26 °C, respectively. The growing season typically begins in mid-March and ends in early-November, lasting ca. 220 days. Mean annual precipitation is 149 cm with no formal dry season (PRISM Climate Group, 2015).

Forests on the Cumberland Plateau are known for having high plant species richness and gamma diversity (Hinkle et al., 1993). Topography and soil-water availability exhibit strong influences on the species composition of plant communities in the region (Hinkle, 1989). The southern Cumberland Plateau is classified as a transition zone between the Mixed Mesophytic Forest region to the north and the *Quercus*–*Pinus* Forest region to the south by Braun (1950). Environmental gradients are steep and stands may contain taxa that would typically dominate at both higher and lower latitudes (Zhang et al., 1999; Richards and Hart, 2011; Parker and Hart, 2014). *Pinus taeda* and *Pinus virginiana* often dominate the ridges and upper slope positions. Less than 100 m down slope of the ridgetops, stands transition to a strong hardwood component as middle and lower slope positions are largely dominated by mesic hardwood species (Zhang et al., 1999; Parker and Hart, 2014). The stands sampled for this study were in the Oak-Pine USDA forest cover type group. Within this cover type, upland hardwoods comprise a plurality of the relative density of tree species, and *Pinus* spp. account for 25–50% relative tree density. This cover type spans millions of hectares with a geographic range from east Texas to the Atlantic coast, and from central Florida to Delaware.

On 20 April 2011, a long-lived bow echo system tracked eastward across northern Alabama (NCDC, 2012). The system produced an EF1 tornado that affected multiple stands within the Bankhead National Forest. The tornado and the winds from the wake low that followed produced wind gusts reaching 153 kph (NWS, 2011). The most heavily impacted areas within the Bankhead National Forest were concentrated in the path of the tornado, while patches of disturbed areas and blowdowns decreased in severity with distance from the swath (Cowden et al., 2014; White et al., 2015; Keasberry et al., 2016; Cox et al., 2016).

2.2. Stand sampling

Stands impacted by the 2011 tornado were surveyed in the fifth growing season post-disturbance. All stands were within the same biophysical setting based on Smalley's (1979) land classification system. An inventory of post-disturbance biophysical conditions was conducted in each stand. A stratified subjective sampling scheme was used to capture the gradient of wind disturbance in the area and categorize effects into severity classes (c.f. Cowden et al., 2014; White et al., 2015). A geo-referenced dataset provided by the USDA Forest Service was used in ArcMap v. 10.2 to determine which stands met the predetermined sampling criteria. The dataset consisted of quantitative information on stand-level species composition, establishment year, roads, established trails, streams, and the tornado damage track. To determine terrain features such as slope and aspect, USGS quadrangles and geo-referenced aerial photographs were imported into ArcMap as basemaps. Using these data, paired with field reconnaissance, stands were selected that: (1) were classified as the Oak-Pine USDA forest cover type, (2) were 40–60 years of age and were artificially regenerated (to represent the age and establishment of most mixed *Pinus*-hardwood stands in the region), (3) were directly affected by the 2011 tornado, and (4) had no recorded or identifiable features indicative of prior exogenous disturbance during stand development. All selected stands ($n = 5$) were directly impacted by the disturbance, but also contained neighborhoods that were not disturbed by the wind event. Undisturbed neighborhoods within stands were used as controls in the study, based on the assumption that they were representative of pre-disturbance conditions using a space-for-time substitution (Cowden et al., 2014; White et al., 2015). Stand boundaries were congruent with those established by management personnel on the Bankhead National Forest.

In ArcMap (Environmental Systems Research Institute, USA) plots were subjectively established in the selected stands to ensure a representative sample distribution across the canopy disturbance gradient based on aerial imagery. Sampled stands contained plots from all disturbance categories. In the field, each predetermined plot identified in ArcMap was visually assessed in the context of surrounding stand conditions. Thus, sample points were established based on a combination of computer mapping and field observation. If the site was deemed suitable after visual assessment, a 0.04 ha fixed-radius overstory vegetation plot was established and classified into one of three severity classes based on the number of downed trees within or crossing through the plot and its proximity to the tornado path (Cowden et al., 2014; White et al., 2015). Plots with three or more downed trees were classified as moderate damage plots (n = 29), and all other plots with visible wind damage (individuals were considered windthrown by the storm if they had been either uprooted so that the stem was less than 45° from the ground or if the bole had been broken below the crown, sensu Canham et al., 2001) were considered to be light disturbance plots (n = 32). Control plots (n = 27) exhibited no visible evidence of damage from the wind event and were located the furthest from the storm track.

2.3. Data collection

For all live woody stems ≥5 cm diameter at breast height (dbh, 1.37 m above the surface) (hereafter referred to as trees), species, dbh, and crown class were recorded. For crown class, each stem was classified as dominant, co-dominant, intermediate, or overtopped based on the amount of intercepted light and height in relation to the adjacent canopy (Oliver and Larson, 1996). Additionally, to further delineate the composition and structure of the subcanopy, the intermediate class was subdivided into intermediate I (I1: <50% of total canopy height), intermediate II (I2: 50–75% of total canopy height), and intermediate III (I3: ≥75% of total canopy height (Cowden et al., 2014; White et al., 2015)). All dead woody stems ≥5 cm dbh rooted within the plot were identified to the lowest possible taxonomic level, measured to estimate standing dbh, assigned a decay class, and categorized as an uprooted stem (root network uplifted), snapped stem (bole broken below the crown), or snag (standing dead tree with intact crown; Clinton et al., 1993; Yamamoto, 2000; Hart and Grissino-Mayer, 2009; Richards and Hart, 2011). To elucidate the influence of the disturbance on overstory composition changes and examine species-specific mortality trends, dead stems were divided into four decay classes based on Fraver et al. (2002): decay class I (sound wood, bark intact, small to medium sized branches present), decay class II (sound to partially rotten wood, branch stubs firmly attached with only larger stubs present, some bark slippage), decay class III (substantially rotten wood, branch stubs easily pulled from softwood species, wood texture is soft and compacts when wet), and decay class IV (mostly rotten wood, branch stubs rotted down to log surface, bark no longer attached or absent, log is oval or flattened in shape). To quantify regeneration patterns, a 40 m^2 plot was established nested within each overstory plot. On these plots, all woody stems <1 m tall were considered seedlings and all stems ≥1 m tall and <5 cm dbh were considered saplings. All seedlings and saplings were tallied by species.

Canopy openness and light regimes at each plot were quantified because light is the abiotic factor most often limiting in closed canopy forests (Oliver and Larson, 1996). For each overstory plot, one hemispherical photograph was taken at breast height at plot center. These photographs were captured by a specialized camera system calibrated by the canopy analysis program (WinSCANOPY, Regent Instruments, Canada) distributor (Wulder, 1998). Two synchronized ceptometers (AccuPAR LP-80, Decagon Devices, USA) were implemented to measure photosynthetically active radiation ($\mu mol\ m^{-2}\ s^{-1}$) (PAR) in the understory; one ceptometer was used to manually record PAR within each plot while a second was placed nearby in full sunlight and set to record automatically (one measurement $minute^{-1}$). On each plot we collected 80 ceptometer measurements at 1.37 m above the surface (20 readings from plot center to plot edge along the cardinal directions). The 80 readings for each plot were averaged to provide a singular value. The mean plot value was divided by the readings simultaneously collected from the full sun ceptometer and converted to determine the percent of full sunlight for each plot.

2.4. Data analyses

To compare the effects of disturbance on composition and structure, all trees (woody stems ≥5 cm dbh) were analyzed by standard descriptors of density (stems ha^{-1}), relative density (contribution to total stems), dominance ($m^2\ ha^{-1}$), relative dominance (contribution to total basal area), and relative importance (average of relative density and relative dominance). Seedlings and saplings were analyzed by density, relative density, frequency (number of plots where the species was present), and relative frequency (percent of plots on which the species was present). We calculated quadratic mean diameter (QMD) and q-factors based on 5 cm dbh bins to analyze diameter distributions across disturbance classes (Nyland, 2002). Species richness (S), abundance, Shannon diversity (H'), and evenness (J') were calculated to determine compositional diversity within each disturbance class. Trees were grouped by genus into four taxonomic groups (*Pinus*, *Quercus*/*Carya*, *Acer*/*Fagus*, and Others) based on similar silvical characteristics relevant to this study (Trimble, 1975).

The decay classification for each tree was used to evaluate the effect of ISD on stand basal area. To account for decay in time since disturbance, the stems considered affected by the storm were softwoods in decay classes II and III, and hardwoods in decay classes I and II (Radtke et al., 2004, 2009). The average percent of basal area removed (i.e. trees killed) within these decay classes in the control plots was used as a surrogate for natural mortality in study stands within the Bankhead National Forest. To account for dead stems that were not killed by the 2011 wind event, the backround rate of mortality was subtracted from basal area of dead stems within these decay class parameters in the light and moderate disturbance classes to estimate the basal area removed by the wind event (sensu Runkle, 1982; Cowden et al., 2014; White et al., 2015). Hereafter in this study, dead stems will only refer to trees within these decay class parameters (i.e. natural mortality in the control class and storm-killed in the light and moderate disturbance classes) because dead stems outside these parameters were determined to have died before or after the disturbance and were not included in our analysis.

Hemispherical photograph analyses were performed using the forest canopy analysis software program WinSCANOPY. All hemispherical photograph analyses were performed by one individual to ensure all images could be directly compared by reducing user bias (Robison and McCarthy, 1999). Each image was analyzed via 'pixel classification', a process of using gray levels to classify each pixel as canopy or sky (Silbernagel and Moeur, 2001; Regent Instruments, 2011). To describe canopy structure and estimate the light environment in the subcanopy, we calculated measures of canopy openness and gap fraction. Gap fraction is the proportion of pixels unobstructed by vegetation on the projected image plane. Canopy openness is similar to gap fraction in that it is the proportion of open sky, but the value assigned to each pixel is adjusted to account for the angular distortion created by the fish-eye lens and weighted in relation to the given zenith angle (Regent Instruments, 2011).

To compare means between the three disturbance classes, all plot-level data were statistically and visually analyzed for normality and homoscedasticity. A one way analysis of variance (ANOVA) test was used to detect differences between means across disturbance classes for all analyses. Where significance ($P < 0.05$) was found, a Scheffe post hoc test was used to distinguish means. Logistic regression was used to predict stem mortality across both disturbance classes. Tree mortality (live v. storm-killed trees) was used as the dependent variable and tree dbh and tree taxonomic group (coded as dummy variables) as independent variables (Trexler and Travis, 1993; Hanson and Lorimer, 2007; Peterson, 2007). The Box-Tidwell transformation was applied to verify a linear relationship between the logit-transformation of tree mortality and dbh, the only continuous independent variable (Menard, 2000). When divided into separate light and moderate disturbance classes, data violated the assumption of linearity. Therefore, we combined data across both disturbance classes to satisfy this assumption and determine taxa- and size-specific mortality trends across all plots disturbed by the wind event. We used the forward selection method with a threshold of $P < 0.05$ to build the model (Peterson, 2007). The likelihood ratio χ^2 was used to test the significance of the model and the wald χ^2 was used to test the significance of variables.

3. Results

3.1. Composition and structure

Mean basal area was statistically different among control, light disturbance, and moderate disturbance classes, with values of 41.8 $m^2\ ha^{-1}$, 33.7 $m^2\ ha^{-1}$, and 21.6 $m^2\ ha^{-1}$, respectively ($P < 0.05$; Table 1). Density of stems $\geq$ 5 cm dbh was 1446 stems ha^{-1} in the control class, 1051 stems ha^{-1} in the light disturbance class, and 968 stems ha^{-1} in the moderate disturbance class. Density was statistically different between the control class and the light and moderate disturbance classes, but not between the light and moderate disturbance classes ($P < 0.05$). Species richness for trees across all classes combined was 41. Mean Shannon diversity of tree species for control plots was 1.91 ± 0.04 (SE), for light disturbance plots was 2.02 ± 0.04, and for moderate disturbance plots was 2.02 ± 0.05. No significant ($P < 0.05$) differences in Shannon diversity or species evenness were noted.

The most important species (based on the mean of relative density and relative dominance) was *P. taeda* (Table 2). In the control class, light disturbance class, and moderate disturbance class importance of *P. taeda* was 44%, 34%, and 26%, respectively. The species with notable increases in total importance with disturbance severity were *Quercus alba, Quercus prinus,* and *Prunus serotina*. Relative density of *Acer rubrum* was slightly higher in the control class than in the light disturbance and moderate disturbance classes because of a larger number of 5–10 cm trees, but there was less than 1% difference in its relative dominance among all three classes (Table 2). Based on importance, *A. rubrum* (13% relative importance) and *P. virginiana* (11%) were the second and third ranked species in the control class. The most important species behind *P. taeda* in the light disturbance class were *A. rubrum* (10%) and *Liriodendron tulipifera* (9%), and in the moderate disturbance class *Q. alba* (15%) and *Q. prinus* (11%).

Size distribution for all live stems resembled a reverse J shape and q-factors in control, light and moderate classes were not significantly different ($P > 0.05$), with mean values of 2.79, 1.88, and 2.13, respectively (Fig. 1). *Pinus* was the only genus that exhibited a unimodal size distribution with *Quercus* spp. and *A. rubrum* both resembling a reverse J. The QMD of live stems was 19 cm ± 0.34, 20 cm ± 0.50, and 17 cm ± 0.55 for control, light, and moderate disturbance classes, respectively. The QMD for *Pinus* was statistically different between light and moderate disturbance classes ($P < 0.05$). The QMD of *Pinus* trees in the control, light disturbance, and moderate disturbance classes was 13, 20, and 24 cm, respectively. The relative density of stems in the I1 canopy class increased from 8% in the control categories to 23% and 35% in the light and moderate disturbance categories, respectively. The relative density of codominant stems decreased from 35% in control to 27% and 15% in the light and moderate disturbance classes, respectively (Fig. 2). In the I3 stratum in the light disturbance class, the combined relative importance values of *P. serotina* and *L. tulipifera,* both considered gap opportunists, was essentially equivalent to *Quercus* spp. (13%). *Quercus* spp. in the moderate disturbance class of this stratum had markedly higher relative importance values (22%) compared to *P. serotina* and *L. tulipifera* (8%). Notably, *A. rubrum* did not increase in dominance in the overtopped or intermediate canopy classes among control and disturbance classes.

3.2. Wind-induced mortality patterns

The storm reduced basal area by approximately 15% in the light disturbance class and 38% in the moderate disturbance class based

Table 1
Mean basal area measures and quadratic mean diameter ± SE for stems ≥5 cm dbh across control (undisturbed), light disturbance, and moderate disturbance classes within wind-disturbed mixed *Pinus*-hardwood stands on the Bankhead National Forest, Alabama, USA. Dead stems in the control class were the result of natural mortality and those in the light and moderate disturbance classes were killed by the storm. Different letters indicate differences at $P < 0.05$.

Parameter		Disturbance class	
	Control	Light	Moderate
Live BA (m^2 0.04 ha $plot^{-1}$)	1.66 ± 0.06 a	1.36 ± 0.06 b	0.87 ± 0.07 c
Live BA ($m^2\ ha^{-1}$)	41.8	33.7	21.6
Dead BA (m2 0.04 ha $plot^{-1}$)	0.08 ± 0.01	0.25 ± 0.02	0.53 ± 0.02
Dead BA (m2 ha^{-1})	2.1	6.0*	12.6*
% BA lost	4.67 ± 0.41 a	15.70 ± 1.04 b	37.88 ± 2.21 c
QMD (cm) of live stems	19.31 ± 0.34 a	20.26 ± 0.50 a	17.00 ± 0.55 b
QMD (cm) of dead stems	11.25 ± 0.48 a	18.39 ± 0.71 b	24.30 ± 0.76 c

* Accounting for background mortality.

Table 2
Density (number of stems ha^{-1}), relative density (contribution to total stems ha^{-1}), dominance (basal area ha^{-1}), and relative dominance (contribution to total basal area) for all live stems ≥5 cm dbh across control (undisturbed), light disturbance, and moderate disturbance classes within wind-disturbed mixed *Pinus*-hardwood stands on the Bankhead National Forest, Alabama. Bankhead National Forest, Alabama, USA. Species were ranked according to the relative dominance in the control class.

Species	Density (stems ha^{-1})			Relative density (%)			Dominance (m^2 ha^{-1})			Relative dominance (%)		
	Control	Light	Moderate	Control	Light	Moderate	Control	Light	Moderate	Control	Light	Moderate
Pinus taeda	377	219	113	26.0	20.9	11.6	26.27	16.27	8.56	62.9	48.3	39.6
Pinus virginiana	144	78	43	10.0	7.4	4.4	5.00	3.25	1.80	12.0	9.6	8.3
Quercus prinus	170	82	102	11.8	7.8	10.6	2.89	2.66	2.37	6.9	7.9	11.0
Liriodendron tulipifera	80	99	24	5.5	9.4	2.5	2.54	3.42	0.58	6.1	10.1	2.7
Acer rubrum	310	178	147	21.4	16.9	15.2	1.50	1.16	0.84	3.6	3.5	3.9
Quercus alba	104	54	144	7.2	5.1	14.8	0.98	2.08	3.34	2.3	6.2	15.4
Quercus rubra	38	5	14	2.6	0.5	1.4	0.80	0.07	0.16	1.9	0.2	0.8
Prunus serotina	28	76	78	1.9	7.2	8.1	0.41	1.25	1.27	1.0	3.7	5.9
Magnolia macrophylla	46	32	19	3.2	3.0	2.0	0.34	0.36	0.18	0.8	1.1	0.8
Quercus velutina	12	12	13	0.8	1.2	1.3	0.25	0.13	0.13	0.6	0.4	0.6
Cornus florida	25	59	49	1.7	5.6	5.1	0.13	0.38	0.32	0.3	1.1	1.5
Nyssa sylvatica	28	30	32	1.9	2.8	3.3	0.12	0.22	0.20	0.3	0.7	0.9
Oxydendron arboreum	14	15	3	1.0	1.4	0.4	0.10	0.15	0.01	0.2	0.4	0.1
Carya tomentosa	21	20	28	1.5	1.9	2.9	0.09	0.19	0.21	0.2	0.6	1.0
Fagus grandifolia	18	22	31	1.2	2.1	3.2	0.08	0.22	0.18	0.2	0.7	0.9
Quercus coccinea	2	6	11	0.1	0.6	1.2	0.07	0.28	0.27	0.2	0.8	1.3
Quercus falcata	6	5	4	0.4	0.5	0.4	0.07	0.29	0.06	0.2	0.8	0.3
Liquidambar styraciflua	1	8	–	0.1	0.7	–	0.05	0.18	–	0.1	0.5	–
Carya glabra	11	18	27	0.8	1.7	2.8	0.03	0.91	0.38	0.1	2.7	1.8
Ilex opaca	4	1	–	0.3	0.1	–	0.01	0.00	–	0.0	0.0	–
Sassafras albidum	2	5	3	0.1	0.4	0.4	0.01	0.04	0.04	0.0	0.1	0.2
Amelanchier arboreum	3	2	5	0.2	0.2	0.5	0.01	0.01	0.02	0.0	0.0	0.1
Diospyros virginiana	1	–	4	0.1	–	0.4	0.00	–	0.05	0.0	–	0.2
Platanus occidentalis	1	–	–	0.1	–	–	0.00	–	–	0.0	–	–
Juniperus virginiana	1	2	5	0.1	0.1	0.5	0.00	0.03	0.10	0.0	0.1	0.5
Ulmus alata	1	1	–	0.1	0.1	–	0.00	0.02	–	0.0	0.1	–
Magnolia acuminata	–	5	3	–	0.4	0.4	–	0.03	0.02	–	0.1	0.1
Fraxinus americanus	–	1	2	–	0.1	0.2	–	0.02	0.00	–	0.1	0.0
Acer saccharum	–	2	8	–	0.2	0.8	–	0.02	0.10	–	0.1	0.5
Fraxinus pennsylvanica	–	3	2	–	0.3	0.2	–	0.01	0.07	–	0.0	0.3
Cercis canadensis	–	2	3	–	0.1	0.4	–	0.01	0.01	–	0.0	0.1
Ostrya virginiana	–	2	38	–	0.1	3.9	–	0.01	0.22	–	0.0	1.0
Fraxinus caroliniana	–	2	–	–	0.2	–	–	0.01	–	–	0.0	–
Quercus stellata	–	2	3	–	0.1	0.4	–	0.00	0.02	–	0.0	0.1
Vaccinium arboreum	–	2	5	–	0.1	0.5	–	0.00	0.01	–	0.0	0.1
Morua rubra	–	1	–	–	0.1	–	–	0.00	–	–	0.0	–
Tilia americana	–	1	–	–	0.1	–	–	0.00	–	–	0.0	–
Carpinus caroliniana	–	1	1	–	0.1	0.1	–	0.00	0.01	–	0.0	0.0
Pinus echinata	–	–	1	–	–	0.1	–	–	0.07	–	–	0.3
Aralia spinosa	–	–	1	–	–	0.1	–	–	0.00	–	–	0.0
Total	1446	1051	968	100.0	100.0	100.0	41.77	33.68	21.61	100.0	100.0	100.0

on values from control plots using a space-for-time substitution. QMD of dead stems was 11 cm ± 0.48, 18 cm ± 0.71, and 23 cm ± 0.76 in the control, light disturbance, and moderate disturbance classes, respectively. Among all dead trees, *Pinus* spp. had the highest density (Fig. 3) and relative density values across the control (21%), light disturbance (27%), and moderate disturbance (35%) classes (Table 3). Logistic regression of tree fate (live stems v. stems killed by the storm) by taxonomic group in the disturbance classes revealed significant probability of mortality for all *Pinus* trees ($P < 0.05$; $\chi^2 < 0.0001$), as well as increasing probability of *Pinus* mortality with diameter ($P < 0.05$; $\chi^2 < 0.0001$; Fig. 4). Probability of other taxonomic groups was not significant. Among all recorded modes of death, uprooted stems exhibited the greatest change in relative density of dead stems from the control class to the light and moderate disturbance classes (3%, 23%, and 30%, respectively; Fig. 5).

3.3. Effects on regeneration and sub-canopy light regimes

Throughout the control and two disturbance classes, 51 unique species were documented within the seedling layer and 45 species were documented in the sapling layer. Density of total stems was statistically different ($P < 0.05$) between the control and disturbance classes in the seedling layer, and among all three classes in the sapling layer. Total seedling density was 28,243, 48,156, and 53,866 ha^{-1}, for control, light, and moderate classes, respectively (Table 4). In the control, light, and moderate classes, sapling density was 1380, 4210, and 6905 ha^{-1}, respectively (Table 5). In the sapling layer, the relative densities of *A. rubrum* and *Quercus* spp. in the disturbance classes averaged 6% and 9% higher than in the control, respectively. *Pinus taeda* seedlings occurred on 74%, 91%, and 83% of plots in the control, light disturbance, and moderate disturbance classes, respectively. In the sapling layer, *P. taeda* stems only occurred on 4% of control plots, and were nonexistent in the light and moderate disturbance classes. *Viburnum acerifolium* occurred on 62% of plots in the moderate disturbance class but only occurred on 9% of plots in the light disturbance class, and was not found at all in the control class. Mean Shannon diversity values per plot within the seedling layer were 1.37 ± 0.08, 1.93 ± 0.07, and 1.79 ± 0.06, and 0.96 ± 0.09, 1.47 ± 0.08, and 1.61 ± 0.09 in the sapling layer for control, light, and moderate classes, respectively. Shannon diversity in the light and moderate disturbance classes was significantly greater than the control class in both the seedling and sapling layers ($P < 0.05$).

Percent full sunlight values calculated from ceptometer readings were significantly ($P < 0.05$) lower in the control class than

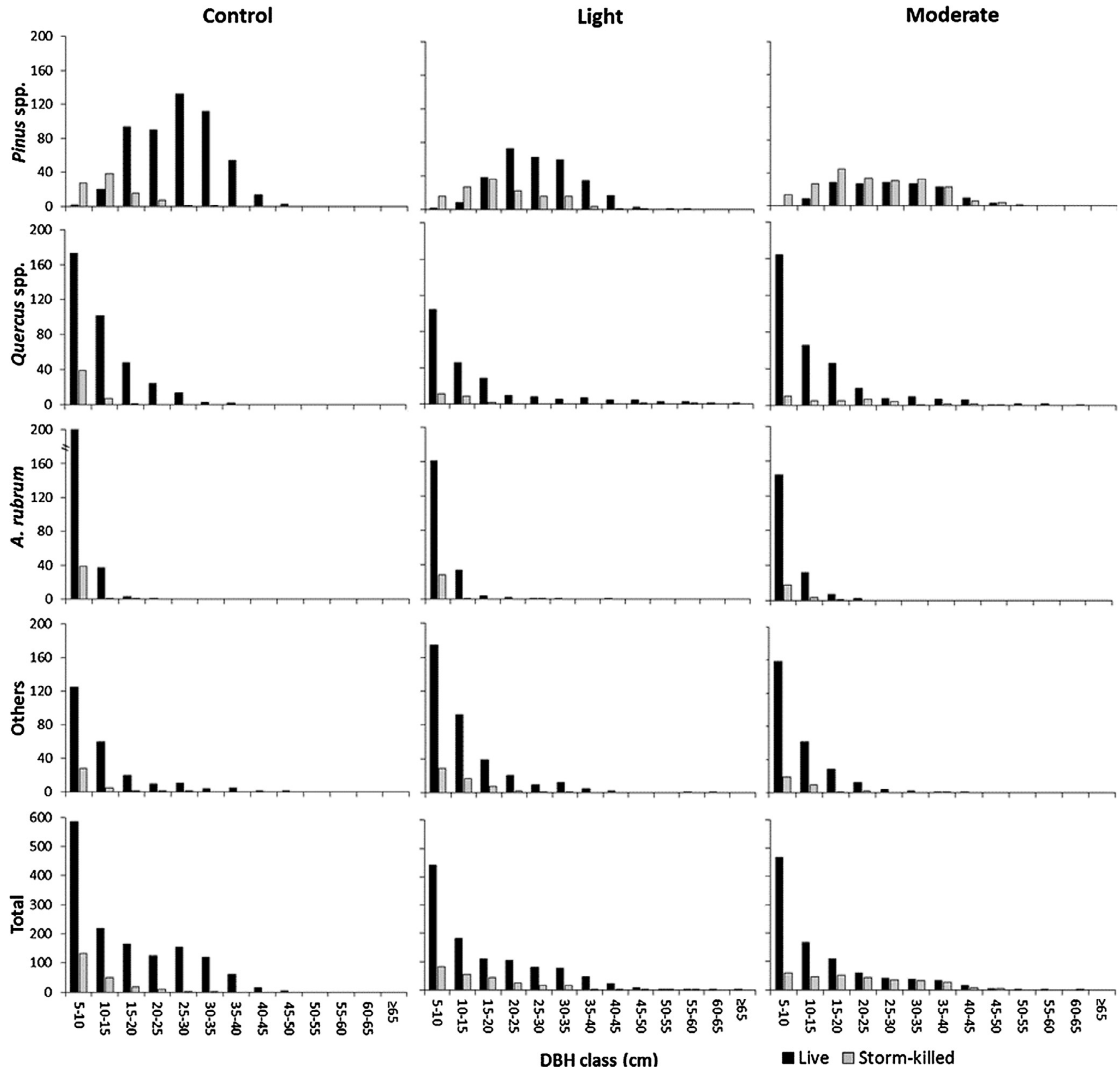

Fig. 1. Density (number of stems ha^{-1}) of live and dead trees in 5 cm diameter bins across control (undisturbed), light disturbance, and moderate disturbance classes within wind-disturbed mixed *Pinus*-hardwood stands on the Bankhead National Forest, Alabama, USA.

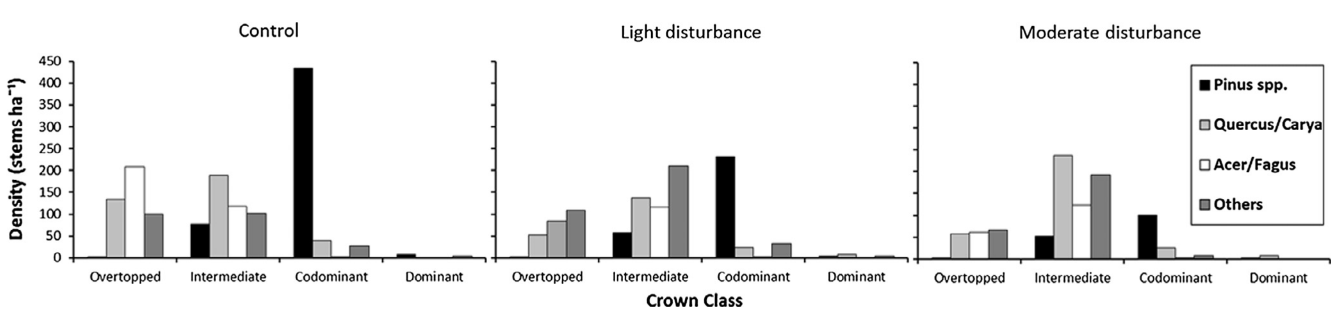

Fig. 2. Density (number of stems ha^{-1}) of stems ≥5 cm dbh grouped by canopy class (based on the amount of intercepted light and height in relation to the adjacent canopy) across control (undisturbed), light disturbance, and moderate disturbance classes within wind-disturbed mixed *Pinus*-hardwood stands on the Bankhead National Forest, Alabama, USA.

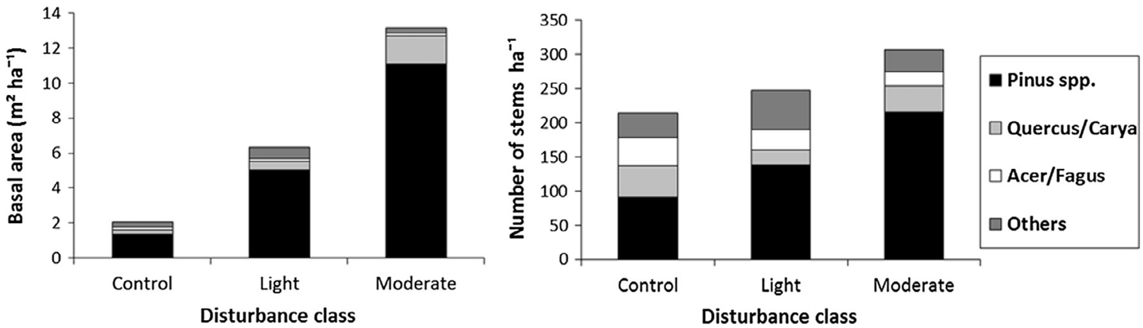

Fig. 3. Basal area and density of dead stems ≥5 cm dbh that were estimated to be killed by an intermediate-severity wind event in the light and moderate disturbance classes, and by natural mortality in the control (undisturbed) class in mixed *Pinus*-hardwood stands on the Bankhead National Forest, Alabama, USA.

Table 3
Density (number of stems ha^{-1}), relative density (proportion of stems ha^{-1}), dominance (basal area ha^{-1}), and relative dominance (proportion of total basal area) for dead stems ≥ 5 cm mixed *Pinus*-hardwood stands on the Bankhead National Forest, Alabama, USA. Dead stems in the control class were the result of natural mortality and those in the light and moderate disturbance classes were killed by the storm. Species were ranked based on relative dominance in the control class.

Species	Density (stems ha^{-1})			Relative Density (%)			Dominance ($m^2\ ha^{-1}$)			Relative Dominance (%)		
	Control	Light	Moderate	Control	Light	Moderate	Control	Light	Moderate	Control	Light	Moderate
Pinus virginiana	30.69	62.40	105.78	14.3	25.2	34.5	0.72	3.33	6.54	35.4	52.7	49.6
Acer rubrum	60.45	73.32	108.36	28.3	29.6	35.3	0.62	1.57	4.53	30.5	24.8	34.4
Pinus taeda	18.60	16.38	4.30	8.7	6.6	1.4	0.20	0.29	0.12	9.9	4.7	0.9
Quercus rubrum	40.92	29.64	21.50	19.1	11.9	7.0	0.17	0.15	0.13	8.4	2.4	1.0
Liriodendron tulipifera	19.53	2.34	4.30	9.1	0.9	1.4	0.13	0.03	0.11	6.2	0.4	0.8
Quercus prinus	14.88	14.82	23.22	7.0	6.0	7.6	0.08	0.43	0.85	3.8	6.7	6.5
Prunus serotina	9.30	21.84	10.32	4.3	8.8	3.4	0.05	0.18	0.11	2.4	2.9	0.9
Quercus alba	8.37	3.12	6.02	3.9	1.3	2.0	0.03	0.04	0.32	1.6	0.6	2.4
Cornus florida	2.79	1.56	3.44	1.3	0.6	1.1	0.01	0.01	0.02	0.5	0.1	0.1
Sassafrass albidum	3.72	3.90	6.02	1.7	1.6	2.0	0.01	0.01	0.03	0.5	0.2	0.2
Magnolia macrophylla	0.93	9.36	1.72	0.4	3.8	0.6	0.01	0.11	0.01	0.3	1.8	0.1
Quercus velutina	0.93	0.78	1.72	0.4	0.3	0.6	0.00	0.00	0.00	0.1	0.1	0.0
Carya glabra	0.93	–	–	0.4	–	–	0.00	–	–	0.1	–	–
Quercus falcata	0.93	–	0.86	0.4	–	0.3	0.00	–	0.24	0.1	–	1.8
Carya tomentosa	0.93	–	0.86	0.4	–	0.3	0.00	–	0.00	0.1	–	0.0
Amelanchier arboreum	–	0.78	–	–	0.3	–	–	0.00	–	–	0.0	–
Diospyros virginiana	–	1.56	–	–	0.6	–	–	0.04	–	–	0.7	–
Fraxinus carolinia	–	0.78	–	–	0.3	–	–	0.00	–	–	0.0	–
Juglans nigra	–	–	0.86	–	–	0.3	–	–	0.01	–	–	0.0
Juniperus virginiana	–	–	2.58	–	–	0.8	–	–	0.03	–	–	0.2
Magnolia acumenata	–	0.78	–	–	0.3	–	–	0.01	–	–	0.1	–
Nyssa sylvatica	–	–	1.72	–	–	0.6	–	–	0.00	–	–	0.0
Oxydendrum arboreum	–	0.78	0.86	–	0.3	0.3	–	0.00	0.01	–	0.0	0.1
Quercus coccinea	–	1.56	0.86	–	0.6	0.3	–	0.01	0.06	–	0.2	0.4
Pinus echinata	–	–	0.86	–	–	0.3	–	–	0.04	–	–	0.3
Pinus spp.	–	2.34	0.86	–	0.9	0.3	–	0.10	0.03	–	1.6	0.2
Total	213.9	248.04	307.02	100	100	100	2.05	6.32	13.18	100	100	100

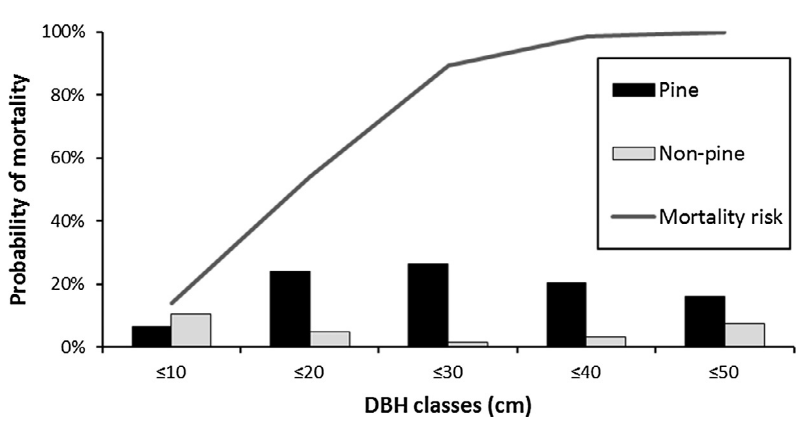

Fig. 4. Logistic regression of mortality by dbh and taxonomic group for live v. storm-killed trees across the combined light and moderate disturbance classes in wind-disturbed stands on the Bankhead National Forest, Alabama, USA. The forward selection method with a threshold of $P < 0.05$ was used to build the model.

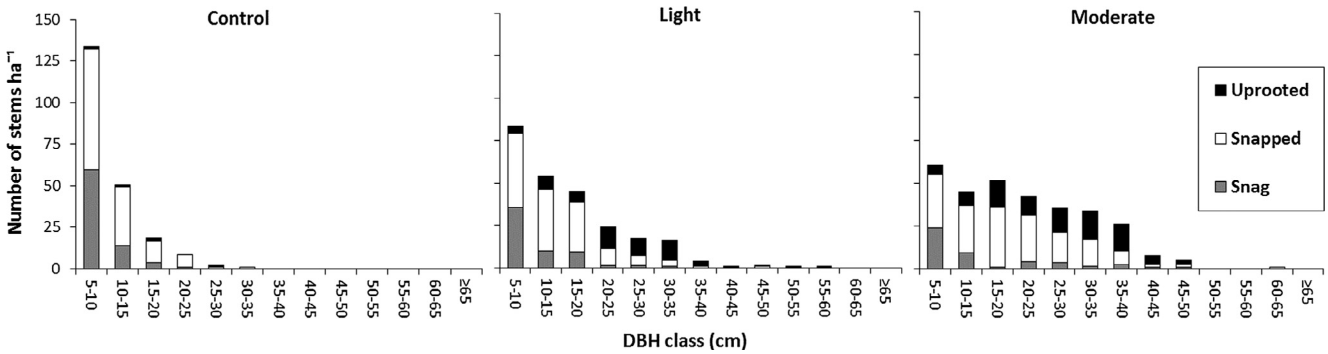

Fig. 5. Mode of death in 5 cm diameter bins for dead stems across the control (undisturbed), light disturbance, and moderate disturbance classes in mixed *Pinus*-hardwood stands on the Bankhead National Forest, Alabama, USA. Dead stems in the control class were the result of natural mortality and those in the light and moderate disturbance classes were killed by the storm.

in the light and moderate disturbance classes and did not differ between the disturbance classes (3% ± 0, 10% ± 2, and 8% ± 1, respectively; $P < 0.05$; Fig. 6). Hemispherical photo analysis yielded gap fraction values of 10% ± 0.57, 11% ± 0.63, and 13% ± 0.69, and percent openness values of 12% ± 0.61, 12% ± 0.67, and 14% ± 0.76 for control, light and moderate classes, respectively. The moderate class exhibited significantly greater values for each of these analyses, but no significant differences were noted between the control and light disturbance classes ($P < 0.05$).

4. Discussion

4.1. Composition and structure

The seedling and sapling layers were dominated by *A. rubrum*, a species able to persist for extended periods under a closed canopy and then recruit to larger size classes following canopy disturbance (Hart et al., 2012b). The high relative frequency of *Pinus* stems in the seedling layer of wind-disturbed stands is evidence of its presence in the seedbed and manifests the capability of the sexually mature *Pinus* stems to produce viable seeds. The general absence of *Pinus* in the sapling layer and its low abundance in the small size classes of the tree layer in the impacted stands indicated the disturbance did not facilitate conditions conducive to the natural regeneration of *Pinus*. Thus, the disturbance may have promoted *Pinus* reproduction, but not recruitment to the sapling layer five growing seasons since the event. Despite their abundance in the seedling layer, the frequency and density of *Quercus* was comparatively low in the sapling layer. This can likely be attributed to an understory light environment below the 20% full sunlight threshold necessary to sustain *Quercus* seedling growth (Dey, 2012). Species such as *A. rubrum* that can persist for extended periods under a closed canopy will likely have a greatest chance of survival under the current disturbance regime (Peterson and Rebertus, 1997; Shelton and Cain, 1999; Hanson and Lorimer, 2001).

The intermediate-severity wind event had the greatest impact on canopy (dominant and codominant crown classes) *Pinus* trees. When grouped into 5 cm diameter bins, stems from all but the largest size class (<1% of all stems) were killed by the storm, yet *Pinus* was the only taxon that was found to have a significant diameter-dependent mortality risk in plots affected by the storm. These results were consistent with prior studies in mixed species stands of the eastern USA that found pioneer cohort *Pinus* stems were more likely to be killed by wind-disturbance than co-occurring hardwoods (Foster 1988; Zimmerman et al., 1994; Batista and Platt, 2003). The disparities in susceptibility to wind-induced mortality were likely attributed to differences in the root and shoot characteristics of the *Pinus* species and co-occurring hardwoods. In general, *Pinus* stems allocate more resources to rapid height growth instead of overall structural strength, making them less wind firm than the slower growing co-occurring hardwoods (Givnish, 1995; USFPL, 1999; Shelton and Cain, 1999) Also, results from prior studies indicate that the susceptibility of *Pinus* stems to wind-damage rapidly increases with tree size (which may be a function of age), but hardwood susceptibility to wind-damage gradually increases with size (Foster, 1988; Foster and Boose, 1992; Peterson and Rebertus, 1997; Shelton and Cain, 1999). This is consistent with canopy tree mortality patterns observed in this study, based on the hypothesis that most canopy hardwoods in the study stands were likely younger and smaller and therefore, more wind-firm as they filled the space made available from the mortality of pioneer cohort *Pinus* stems. The wind event documented here occurred in late-April and the deciduous trees had fully developed foliage at this time. We note that a similar wind event during leaf-off conditions may have resulted in different patterns. White et al. (2015) and Cox et al. (2016) examined mortality patterns caused by the same EF1 tornado in hardwood-dominated stands and found significant positive relationships between tree diameter and mortality probability.

The theoretical basis for successional pathways in mixed *Pinus*-hardwood stands in the eastern USA has been established; during stand initiation, early-seral *Pinus* stems grow fast and dominate, but they cannot regenerate in the low light environment of a closed canopy (Glitzenstein et al., 1986; Peet and Christensen, 1980; Cooper, 1989). This allows more shade tolerant hardwoods to establish and persist in the understory until canopy space is made available from the mortality of pioneer cohort *Pinus* stems. Historically, natural mixed *Pinus*-hardwood systems were likely maintained by periodic fires severe enough to kill the majority of shade-tolerant hardwoods in the understory (at least top kill), allowing *Pinus* to naturally regenerate (Braun, 1950; Cowell, 1998; Clabo and Clatterbuck, 2015). In the absence of fire, disturbance regimes characterized by gap-scale disturbance events may predominate (Abrams, 1998; Weber et al., 2014). These gap-scale events are typically associated with the establishment and recruitment of mid- to late-successional species, eventually leading to pure stands of hardwoods (Braun, 1950; Cooper, 1989; Shelton and Cain, 1999; Schweitzer and Dey, 2011; Weber et al., 2014). *Pinus* stands in the region reportedly enter the understory reinitiation stage of development around 50–60 years after establishment (Peet and Christensen, 1980; Oliver and Larson, 1996). Prior to the wind disturbance, the stands sampled were in the understory reinitiation stage of development based on stand age and findings from the undisturbed neighborhoods. Wind disturbances, such that impacted the stands here, typically benefit the mid- to late-successional hardwood species that established prior

Table 4
Density (number of stems ha^{-1}), relative density (contribution to stems ha^{-1}), frequency (number of plots on which each species occurred), and relative frequency (contribution to total occurrence) for all seedlings ($\geq$ 1 m height, $\leq$5 cm dbh) across the control, light disturbance, and moderate disturbance classes of wind-disturbed, mixed *Pinus*-hardwood stands on the Bankhead National Forest, Alabama, USA. Species were ranked based on relative density in the control class.

Species	Density (stems/ha)			Relative density (%)			Frequency (# plots)			Relative frequency (%)		
	Control	Light	Moderate	Control	Light	Moderate	Control	Light	Moderate	Control	Light	Moderate
Acer rubrum	15881	14894	11671	56.2	30.9	21.7	27	32	28	100.0	100.0	96.6
Pinus taeda	2759	4389	1862	9.8	9.1	3.5	20	29	24	74.1	90.6	82.8
Vaccineum spp.	1454	3967	7879	5.1	8.2	14.6	12	23	23	44.4	71.9	79.3
Quercus rubra	1028	906	836	3.6	1.9	1.6	19	29	24	70.4	90.6	82.8
Viburnum acerifolium	1009	2156	13025	3.6	4.5	24.2	9	15	26	33.3	46.9	89.7
Prunus serotina	917	2851	3879	3.2	5.9	7.2	23	31	23	85.2	96.9	79.3
Quercus prinus	889	859	802	3.1	1.8	1.5	16	19	16	59.3	59.4	55.2
Quercus alba	565	2374	2500	2.0	4.9	4.6	19	28	25	70.4	87.5	86.2
Nyssa sylvatica	537	812	310	1.9	1.7	0.6	12	14	13	44.4	43.8	44.8
Quercus velutina	463	836	181	1.6	1.7	0.3	13	21	13	48.1	65.6	44.8
Sassafras albidum	426	2452	1353	1.5	5.1	2.5	9	17	18	33.3	53.1	62.1
Carya tomentosa	407	883	983	1.4	1.8	1.8	14	23	23	51.9	71.9	79.3
Frangula caroliniana	370	3304	2767	1.3	6.9	5.1	17	23	16	63.0	71.9	55.2
Liriodendron tulipifera	315	1539	414	1.1	3.2	0.8	14	20	16	51.9	62.5	55.2
Carya globera	278	976	1250	1.0	2.0	2.3	15	29	27	55.6	90.6	93.1
Diospyros virginiana	194	648	336	0.7	1.3	0.6	10	19	13	37.0	59.4	44.8
Asimina triloba	148	203	328	0.5	0.4	0.6	8	10	13	29.6	31.3	44.8
Rhamnus cathartica	93	836	233	0.3	1.7	0.4	1	3	2	3.7	9.4	6.9
Ostrya viginiana	93	266	500	0.3	0.6	0.9	4	10	8	14.8	31.3	27.6
Magnolia macrophylla	74	125	103	0.3	0.3	0.2	5	10	6	18.5	31.3	20.7
Americana arboreum	74	94	241	0.3	0.2	0.4	3	7	11	11.1	21.9	37.9
Cornus florida	46	273	414	0.2	0.6	0.8	2	11	9	7.4	34.4	31.0
Fagus grandifolia	37	141	78	0.1	0.3	0.1	3	6	4	11.1	18.8	13.8
Callicarpa americana	37	94	–	0.1	0.2	–	2	5	–	7.4	15.6	–
Quercus falcata	28	187	233	0.1	0.4	0.4	2	7	11	7.4	21.9	37.9
Styrax grandifolius	28	55	–	0.1	0.1	–	3	2	–	11.1	6.3	–
Oxydendron arboreum	28	8	9	0.1	0.0	0.0	2	1	1	7.4	3.1	3.4
Styrax americanus	28	–	–	0.1	–	–	1	–	–	3.7	–	–
Fraxinus pennsylvanica	9	578	250	0.0	1.2	0.5	1	7	9	3.7	21.9	31.0
Liquidambar styraciflua	9	383	–	0.0	0.8	–	1	2	–	3.7	6.3	–
Ulmus alata	9	47	–	0.0	0.1	–	1	2	–	3.7	6.3	–
Ilex opaca	9	23	17	0.0	0.0	0.0	1	3	2	3.7	9.4	6.9
Hydrangea quercifolia	–	234	216	–	0.5	0.4	–	6	7	–	18.8	24.1
Quercus stellata	–	164	112	–	0.3	0.2	–	6	6	–	18.8	20.7
Euonymus americanus	–	141	172	–	0.3	0.3	–	4	4	–	12.5	13.8
Magnolia acuminata	–	86	9	–	0.2	0.0	–	2	1	–	6.3	3.4
Forestiera ligustrina	–	86	–	–	0.2	–	–	1	–	–	3.1	–
Quercus coccineum	–	55	233	–	0.1	0.4	–	3	8	–	9.4	27.6
Fraxinus americana	–	55	78	–	0.1	0.1	–	4	4	–	12.5	13.8
Acer saccharum	–	39	86	–	0.1	0.2	–	3	4	–	9.4	13.8
Cercis canadensis	–	39	86	–	0.1	0.2	–	4	3	–	12.5	10.3
Aralia spinosa	–	23	129	–	0.0	0.2	–	1	5	–	3.1	17.2
Crataegus spp.	–	23	43	–	0.0	0.1	–	2	3	–	6.3	10.3
Morus rubra	–	16	9	–	0.0	0.0	–	1	1	–	3.1	3.4
Carpinus caroliniana	–	8	9	–	0.0	0.0	–	1	1	–	3.1	3.4
Sambucus spp.	–	8	–	–	0.0	–	–	1	–	–	3.1	–
Elaeagnus spp.	–	8	–	–	0.0	–	–	1	–	–	3.1	–
Kalmia latifolia	–	–	190	–	–	0.4	–	–	1	–	–	3.4
Juglans nigra	–	–	17	–	–	0.0	–	–	2	–	–	6.9
Acer barbatum	–	–	9	–	–	0.0	–	–	1	–	–	3.4
Rubus spp.	–	–	9	–	–	0.0	–	–	1	–	–	3.4
Grand total	28,243	48,140	53,857	100.0	100.0	100.0	–	–	–	–	–	–

to the canopy disturbance event (Abrams and Scott, 1989; Franklin el al., 2007; Xi et al., 2008). Because the ISD primarily removed pioneer cohort *Pinus* stems, and hardwood dominance in the midstory increased with disturbance severity, the wind event resulted in disturbance-mediated accelerated succession (Foster, 1988; Abrams and Scott, 1989; Shelton and Cain, 1999). Post-disturbance dynamics are in part a function of the stand's pre-disturbance status in the understory reinitiation stage of development (i.e., the wind-event resulting in disturbance-mediated accelerated succession is likely a product of the well-developed midstory). This result is consistent with prior ISD studies in stands in the understory reinitiation stage of development (Woods, 2004; Johnson et al., 2009; Holzmueller et al., 2012; White et al., 2015).

Throughout the studied stands, the wind event created a patchwork mosaic of canopy disturbance with single and multi-treefall gaps, areas with few standing trees, and clusters of undamaged trees within the broader matrix of disturbance. This non-uniform distribution of damage is, in part, a function of the dissimilar vertical strata that are characteristic of the understory reinitiation stage of stand development (Franklin et al., 2007; Johnson et al., 2009; Cowden et al., 2014). The unique stand structures created by the disturbance were outside the four distinct stages of stand development as described by Oliver and Larson (1996). Thus, we suggest the "mixed-stage" of stand development, described in Johnson et al. (2009), best embodies the resultant structural state of the stands after the intermediate wind-disturbance. The mixed-stage of development results from an incomplete stand-

Table 5
Density (number of stems ha^{-1}), relative density (contribution to stems ha^{-1}), frequency (number of plots on which each species occurred), and relative frequency (contribution to total occurrence) for all saplings (≥1 m height, ≤5 cm dbh) across the control, light disturbance, and moderate disturbance classes of wind-disturbed, mixed *Pinus*-hardwood stands on the Bankhead National Forest, Alabama, USA. Species were ranked based on relative density in the control class.

Species	Density (stems/ha)			Relative density (%)			Frequency (# plots)			Relative frequency (%)		
	Control	Light	Moderate	Control	Light	Moderate	Control	Light	Moderate	Control	Light	Moderate
Acer rubrum	482	1125	2215	34.9	26.7	32.1	19	31	28	70.4	96.9	96.6
Nyssa sylvatica	176	164	95	12.8	3.9	1.4	7	12	8	25.9	37.5	27.6
Carya tomentosa	148	172	328	10.7	4.1	4.7	11	14	15	40.7	43.8	51.7
Carya glabra	139	164	241	10.1	3.9	3.5	13	10	16	48.1	31.3	55.2
Fraxinus caroliniana	65	500	543	4.7	11.9	7.9	3	12	12	11.1	37.5	41.4
Quercus prinus	46	148	284	3.4	3.5	4.1	4	9	14	14.8	28.1	48.3
Quercus alba	37	148	371	2.7	3.5	5.4	4	10	15	14.8	31.3	51.7
Liriodendron tulipifera	37	148	26	2.7	3.5	0.4	3	5	3	11.1	15.6	10.3
Magnolia macrophylla	37	78	69	2.7	1.9	1.0	2	4	5	7.4	12.5	17.2
Oxydendron arboreum	37	16	43	2.7	0.4	0.6	2	2	4	7.4	6.3	13.8
Vaccinium spp.	28	141	181	2.0	3.3	2.6	3	5	9	11.1	15.6	31.0
Asimina triloba	28	23	69	2.0	0.6	1.0	3	2	6	11.1	6.3	20.7
Ilex opaca	28	23	34	2.0	0.6	0.5	2	2	4	7.4	6.3	13.8
Prunus serotina	19	39	9	1.3	0.9	0.1	2	4	1	7.4	12.5	3.4
Fagus grandifolia	19	31	95	1.3	0.7	1.4	2	4	8	7.4	12.5	27.6
Sassafras albidum	9	297	284	0.7	7.1	4.1	1	8	8	3.7	25.0	27.6
Quercus velutina	9	86	129	0.7	2.0	1.9	1	7	9	3.7	21.9	31.0
Diospyros virginiana	9	23	43	0.7	0.6	0.6	1	3	4	3.7	9.4	13.8
Hydrangea quercifolia	9	23	9	0.7	0.6	0.1	1	2	1	3.7	6.3	3.4
Liquidambar styraciflua	9	–	–	0.7	–	–	1	–	–	3.7	–	–
Pinus taeda	9	–	–	0.7	–	–	1	–	–	3.7	–	–
Fraxinus pennsylvanica	–	164	52	–	3.9	0.7	–	5	5	–	15.6	17.2
Cornus florida	–	109	52	–	2.6	0.7	–	3	6	–	9.4	20.7
Ostrya virginiana	–	102	319	–	2.4	4.6	–	8	7	–	25.0	24.1
Quercus rubra	–	102	259	–	2.4	3.7	–	8	12	–	25.0	41.4
Styrax grandifolius	–	62	–	–	1.5	–	–	2	–	–	6.3	–
Euonymus americanus	–	55	–	–	1.3	–	–	1	–	–	3.1	–
Quercus coccinea	–	47	26	–	1.1	0.4	–	3	3	–	9.4	10.3
Viburnum acerifolium	–	39	750	–	0.9	10.9	–	3	18	–	9.4	62.1
Amelianchier arborea	–	39	147	–	0.9	2.1	–	4	8	–	12.5	27.6
Quercus stellata	–	31	17	–	0.7	0.2	–	1	1	–	3.1	3.4
Fraxinus americana	–	16	34	–	0.4	0.5	–	2	2	–	6.3	6.9
Juniperus virginiana	–	16	–	–	0.4	–	–	2	–	–	6.3	–
Forestiera ligustrina	–	16	–	–	0.4	–	–	1	–	–	3.1	–
Quercus falcata	–	8	52	––	0.2	0.7	–	1	4	–	3.1	13.8
Acer saccharum	–	8	26	–	0.2	0.4	–	1	3	–	3.1	10.3
Aralia spinosa	–	8	17	–	0.2	0.2	–	1	2	–	3.1	6.9
Magnolia acuminata	–	8	17	–	0.2	0.2	–	1	1	–	3.1	3.4
Ulmus alata	–	8	17	–	0.2	0.2	–	1	2	––	3.1	6.9
Cercis canadensis	–	8	9	–	0.2	0.1	–	1	1	–	3.1	3.4
Morus rubra	–	8	–	–	0.2	–	–	1	–	–	3.1	–
Crataegus spp.	–	8	–	–	0.2	–	–	1	–	–	3.1	–
Rhamnus cathartica	–	–	26	–	–	0.4	–	–	1	–	–	3.4
Callicarpa americana	–	–	9	–	–	0.1	–	–	1	–	–	3.4
Rhus copalinum	–	–	9	–	–	0.1	–	–	1	–	–	3.4
Total	1380	4210	6905	100.0	100.0	100.0	–	–	–	–	–	–

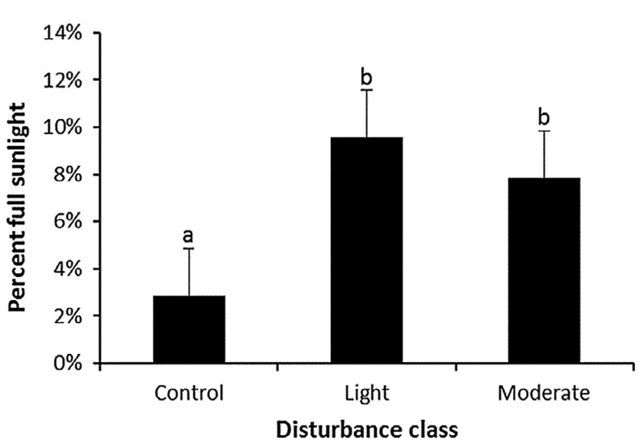

Fig. 6. Mean (with standard error) percent of full sunlight values for control (undisturbed), light disturbance, and moderate disturbance classes within wind-disturbed, mixed *Pinus*-hardwood stands on the Bankhead National Forest, Alabama, USA. Bars with different letters were significantly different ($P < 0.05$).

scale disturbance that results in irregularly spaced populations of younger trees developing in canopy openings mixed with patches of residual, older trees. In the absence of disturbances more severe than localized canopy gaps, the stands may advance to the complex stage of stand development. The complex stage is characterized by a reverse J-shaped diameter distribution with a multiple-aged canopy (Oliver and Larson, 1996; Johnson et al., 2009).

4.2. Light regimes and diversity

We noted a significant difference between undisturbed and disturbed neighborhoods for all three variables tested to assess understory light regimes five growing seasons after an intermediate scale wind-disturbance. Gap fraction and canopy openness were significantly greater in the moderate disturbance class than in the control class. Although significant differences were found between the control class and moderate disturbance class, this is not necessarily indicative of a closed canopy in the light disturbance class, but rather that midstory trees likely increased enough in height and crown volume to sufficiently abrogate any increases in light from canopy gaps caused by the wind disturbance. Percent of full sunlight was significantly greater in both the light and moderate disturbance classes than in the control class five years after the storm. Cowden et al. (2014) found that moderately disturbed neighborhoods had significantly higher insolation levels than undisturbed neighborhoods three growing seasons after an intermediate-wind event in adjacent hardwood-dominated stands. Prior to the disturbance (based on our control plots), the midstory of our study stands was well-developed with trees in the intermediate position accounting for 33% of all stems in the control class. In the light and moderate disturbance classes, the relative density of trees in the intermediate canopy position was 48% and 65%, respectively. Thus, rather than allowing for the establishment of new stems, the disturbance largely served as a mechanism to release the stems already present in the midstory (i.e. disturbance mediated succession; Abrams and Scott, 1989; Holzmueller et al., 2012; Cowden et al., 2014). This result is, in part, a function of the stand's developmental status in the understory reinitiation stage of development at the time of disturbance. We posit that had the disturbance impacted the stands during stem exclusion of the pioneer cohort *Pinus* stems, an earlier stage of stand development, the regeneration and recruitment patterns in the understory may have been different. Although the canopy trees and, consequently, the canopy openings may have been smaller after a disturbance during the stem exclusion stage, without a well-developed midstory, the higher light levels induced by the disturbance may have endured for a longer period in openings too large to be closed by lateral crown expansion. This may have allowed the shade-intolerant *Pinus* spp. the opportunity to regenerate and recruit to the canopy (Woods, 2004; Johnson et al., 2009; Weber et al., 2014).

Within the tree layer, no discernible difference in species diversity (*H*') was present between the control class and the light and moderate disturbance classes or between the disturbance classes individually. However, species diversity values in both the seedling and sapling layers were significantly greater from the control class to the light and moderate disturbance classes. These results were consistent with prior studies that found higher levels of tree diversity in the understory, but not among canopy trees following moderate-severity wind disturbances (Foster, 1988; Peterson and Rebertus, 1997; Cowden et al., 2014). One explanation for these findings may be time since disturbance; seedlings present at the time of the wind-event were able to recruit to the sapling layer, propagules in the seedbed and those that arrived shortly thereafter were able to germinate and become seedlings and saplings, but five growing seasons may not be enough time for the disturbance to drive a significant change in diversity of the overstory (Xi et al., 2008). Additionally, the abundance of residual midstory stems may have mitigated much of the possible impact the disturbance may have otherwise had on tree level diversity by preventing the recruitment of saplings and small trees (Batista et al., 1998; Batista and Platt, 2003; Woods, 2004). Once the well-established understory or midstory stems fill the available space by vertical and/or lateral crown extension, most shade-intolerant and moderately tolerant seedlings and saplings that established in the open conditions that immediately followed the disturbance will not be able to survive. This may ultimately cause any significant increases in diversity to be transitory and restricted to the regeneration layer (e.g. Holzmueller et al., 2012; Cowden et al., 2014; Vodde et al., 2015).

4.3. Management implications

Forest managers in the eastern USA and elsewhere are increasingly being tasked with maintaining a *Pinus* component in stands that would naturally succeed to hardwood dominance, or conversely, promoting a hardwood component in *Pinus* dominated stands by accelerating succession. If a *Pinus* component is to be retained in successional stands, disturbances that create conditions that favor *Pinus* regeneration and recruitment must be created through silvicultural treatments (Cooper, 1989; Clabo and Clatterbuck, 2015). The requirements for *Pinus* regeneration in *Pinus*-hardwood stands include canopy openings that provide sufficient light to seedling and sapling sized *Pinus* stems, and for the species documented here *P. taeda*, *P. echinata*, and *P. virginiana*, a seedbed of exposed mineral soil is required or favorable (Fowells, 1965; Trimble, 1975). One approach to maintain a *Pinus* component in stands that are transitioning to hardwood dominance is to strategically create group openings throughout the stands that are focused on existing patches of *Pinus* advanced reproduction.

If *Pinus* advanced reproduction is absent from the stand, outplantings of *Pinus* seedlings in the group openings may be used. Regardless if natural or artificial regeneration is used, position of the canopy openings should take intra-stand patterns into consideration and be focused on sites with abiotic conditions hypothesized to favor *Pinus* regeneration (e.g. xeric and subxeric microsites). *Pinus* reproduction grows best in full sunlight and harvest-created openings should be sufficiently large to provide such conditions (Jackson, 1959, 1962). Thus, the size of the openings should be scaled in accord with site factors, such as the size of the regeneration patch and the height of trees surrounding the opening. Where present, residual *Pinus* stems should be retained within the openings. Hardwood stems that are less than 1.5 m tall may remain as they will likely be overtopped by the faster growing *Pinus* trees (Chapman, 1945), but residual basal area in the openings should not exceed 17 $m^2\ ha^{-1}$ and may be much lower (Cain, 1993; Murphy et al., 1993; Shelton and Murphy, 1994; Shelton and Cain, 2000). Timing the group openings in conjunction with good *Pinus* seed crops may help secure abundant reproduction (Shelton and Murphy, 1994). On sites where sexually mature *Pinus* trees are scarce, outplanting *Pinus* seedlings in openings at spacings up to 3×3 m is an available option following site preparation (Phillips and Abercrombie, 1987; Waldrop, 1997). If resources allow, tighter spacings should help control for competition. On xeric and subxeric sites, the use of herbicide to control hardwood competition may be an option to allow *Pinus* seedlings to establish and recruit to larger size classes (Zedaker et al., 1989; Waldrop, 1997; Schweitzer and Dey, 2011).

The intermediate-severity wind event documented here did not result in *Pinus* regeneration, but accelerated succession toward hardwood dominance. On sites with abundant hardwood advanced reproduction, canopy disturbance alone is insufficient to regenerate shade-intolerant *Pinus* species. A combination of fire or herbicide application that removes understory stems and wind events that create openings sufficiently large to allow for establishment of shade-intolerant *Pinus*, may produce the necessary site conditions that allow *Pinus* to regenerate. Based on their relative importance in the midstory of stands impacted by the storm, *Quercus* spp., *P. serotina*, and *L. tulipifera* will constitute the majority of the second cohort of canopy trees in the stands documented here. However, based on abundance in the understory, with a gap-scale disturbance regime, *A. rubrum*, and to a lesser extent *Carya* spp., are also likely to become more important canopy components (Barden, 1980; Abrams, 1998; Woods, 2004; Hart et al., 2012b; Cowden et al., 2014).

Conversely, in pure or mostly pure *Pinus* stands, such as *Pinus* plantations, a management objective may be to establish and/or promote a hardwood component to achieve a mixed *Pinus*-hardwood system, as in Schweitzer et al. (2013). Both the natural and managed disturbance events analyzed here effectively accelerated succession by removing overstory *Pinus* stems and releasing hardwood advanced reproduction that was established prior to canopy disturbance. We note that, characteristic of most intermediate-severity disturbances, the wind-event documented here did not impact any of the stands uniformly; rather the stands contained canopy openings across a range of sizes and included undamaged neighborhoods in the broader matrix of disturbance. Variable density thinning, which purposefully promotes structural heterogeneity (Franklin et al., 2007), may be the most appropriate strategy to emulate the patchwork mosaic of canopy openings characteristic of ISD events that may accelerate succession toward hardwood dominance in *Pinus* stands with an abundance of hardwood advanced reproduction.

Acknowledgements

This research was funded as a Joint Venture Agreement between the Northern Research Station, USDA Forest Service and the University of Alabama. We thank Lauren Cox, Jonathan Kleinman, Kathryn Mullen, and Cynthia Taylor for assistance in the field, the Bankhead National Forest staff for logistical support, and two referees for thoughtful comments on a prior draft of the manuscript.

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