12-5-2009

Windthrow and salvage logging in an old-growth hemlock-northern hardwoods forest

Katharyn D. Lang
Iowa State University

Lisa A. Schulte
Iowa State University, lschulte@iastate.edu

Glenn R. Guntenspergen
United States Geological Survey

Windthrow and salvage logging in an old-growth hemlock-northern hardwoods forest

Abstract

Although the initial response to salvage (also known as, post-disturbance or sanitary) logging is known to vary among system components, little is known about longer term forest recovery. We examine forest overstory, understory, soil, and microtopographic response 25 years after a 1977 severe wind disturbance on the Flambeau River State Forest in Wisconsin, USA, a portion of which was salvage logged. Within this former old-growth hemlock-northern hardwoods forest, tree dominance has shifted from Eastern hemlock (*Tsuga canadensis*) to broad-leaf deciduous species (*Ulmus americana*, *Acer saccharum*, *Tilia americana*,*Populus tremuloides*, and *Betula alleghaniensis*) in both the salvaged and unsalvaged areas. While the biological legacies of pre-disturbance seedlings, saplings, and mature trees were initially more abundant in the unsalvaged area, regeneration through root suckers and stump sprouts was common in both areas. After 25 years, tree basal area, sapling density, shrub layer density, and seedling cover had converged between unsalvaged and salvaged areas. In contrast, understory herb communities differed between salvaged and unsalvaged forest, with salvaged forest containing significantly higher understory herb richness and cover, and greater dominance of species benefiting from disturbance, especially *Solidago* species. Soil bulk density, pH, organic carbon content, and organic nitrogen content were also significantly higher in the salvaged area. The structural legacy of tip-up microtopography remains more pronounced in the unsalvaged area, with significantly taller tip-up mounds and deeper pits. Mosses and some forest herbs, including*Athyrium filix-femina* and *Hydrophyllum virginianum*, showed strong positive responses to this tip-up microrelief, highlighting the importance of these structural legacies for understory biodiversity. In sum, although the pathways of recovery differed, this forest appeared to be as resilient to the compound disturbances of windthrow plus salvage logging as to wind disturbance alone, by most vegetative measures.

Keywords

wind, post-disturbance logging, sanitary logging, forest recovery, microtopography, tip-up, Flambeau River, Wisconsin

Disciplines

Forest Management | Natural Resources Management and Policy

Comments

This article is from *Forest Ecology and Management* 259, no. 1 (2008): 56–64, doi:10.1016/j.foreco.2009.09.042.

Forest Ecology and Management 259 (2009) 56–64

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Windthrow and salvage logging in an old-growth hemlock-northern hardwoods forest

Katharyn D. Lang [a,*], Lisa A. Schulte [a], Glenn R. Guntenspergen [b]

[a] Natural Resource Ecology and Management, Iowa State University, 339 Science II, Ames, IA 50011-3221, USA
[b] U.S. Geological Survey/Patuxent Wildlife Research Center, Laurel, MD 20708, USA

ARTICLE INFO

Article history:
Received 20 April 2009
Received in revised form 22 September 2009
Accepted 24 September 2009

Keywords:
Wind
Post-disturbance logging
Sanitary logging
Forest recovery
Microtopography
Tip-up
Flambeau River
Wisconsin

ABSTRACT

Although the initial response to salvage (also known as, post-disturbance or sanitary) logging is known to vary among system components, little is known about longer term forest recovery. We examine forest overstory, understory, soil, and microtopographic response 25 years after a 1977 severe wind disturbance on the Flambeau River State Forest in Wisconsin, USA, a portion of which was salvage logged. Within this former old-growth hemlock-northern hardwoods forest, tree dominance has shifted from Eastern hemlock (*Tsuga canadensis*) to broad-leaf deciduous species (*Ulmus americana*, *Acer saccharum*, *Tilia americana*, *Populus tremuloides*, and *Betula alleghaniensis*) in both the salvaged and unsalvaged areas. While the biological legacies of pre-disturbance seedlings, saplings, and mature trees were initially more abundant in the unsalvaged area, regeneration through root suckers and stump sprouts was common in both areas. After 25 years, tree basal area, sapling density, shrub layer density, and seedling cover had converged between unsalvaged and salvaged areas. In contrast, understory herb communities differed between salvaged and unsalvaged forest, with salvaged forest containing significantly higher understory herb richness and cover, and greater dominance of species benefiting from disturbance, especially *Solidago* species. Soil bulk density, pH, organic carbon content, and organic nitrogen content were also significantly higher in the salvaged area. The structural legacy of tip-up microtopography remains more pronounced in the unsalvaged area, with significantly taller tip-up mounds and deeper pits. Mosses and some forest herbs, including *Athyrium filix-femina* and *Hydrophyllum virginianum*, showed strong positive responses to this tip-up microrelief, highlighting the importance of these structural legacies for understory biodiversity. In sum, although the pathways of recovery differed, this forest appeared to be as resilient to the compound disturbances of windthrow plus salvage logging as to wind disturbance alone, by most vegetative measures.

Published by Elsevier B.V.

1. Introduction

Salvage logging, also known as post-disturbance or sanitary logging, after a major natural disturbance is controversial within forest science and management. Salvage logging removes commercially valuable timber from a stand after a natural disturbance such as fire or windthrow. Some of the debate stems from the lack of a clear response as impacts differ based on (1) the type, magnitude, and conditions leading up to the natural disturbance, (2) the timing and intensity of the salvage harvest, and (3) the ecosystem component studied (van Nieuwstadt et al., 2001; Elliott et al., 2002; Beschta et al., 2004). A recent review of the salvage logging literature organizes these impacts into the broad categories of "altered stand structural complexity; altered ecosystem processes and functions; and altered populations of species and community composition" (Lindenmayer and Noss, 2006). But because these forest components are also altered by natural disturbances, the degree to which the combined impacts of natural disturbance and salvage logging extend beyond those of natural disturbance alone is of substantial concern. The critical question is whether compound disturbances create novel conditions which alter forest recovery. In such cases the consequence may be an "ecological surprise" to which few organisms are adapted (Paine et al., 1998), and hence a high potential for subsequent loss in biodiversity and productivity. While several studies conducted in forest salvaged after fire suggest that salvage logging creates ecologically novel conditions (van Nieuwstadt et al., 2001; Donato et al., 2006; Lindenmayer and Ough, 2006), few studies have assessed the impacts of salvage logging following other types of forest disturbance.

Here we examine the particular case of salvage logging following high severity wind disturbance. High severity winds are common in many forest regions throughout the U.S.

* Corresponding author at: U.S. Forest Service Northern Research Station, 1831 Highway 169E, Grand Rapids, MN 55744, USA. Tel.: +1 218 326 7136.
E-mail address: katharynlang@fs.fed.us (K.D. Lang).

0378-1127/$ – see front matter. Published by Elsevier B.V.
doi:10.1016/j.foreco.2009.09.042

(Cooper-Ellis et al., 1999; Sinton et al., 2000; Batista and Platt, 2003; Schulte and Mladenoff, 2005), as well as in Europe and the Caribbean (Ulanova, 2000; Fischer et al., 2002; Boose et al., 2004). By definition, severe windthrow in forest systems causes abundant treefalls, especially within large tree size classes, and thereby alters the size structure of the forest (Peterson, 2000). Environmental conditions, including the spatial distribution of light, microrelief of the forest floor through tree tip-ups, and spatial heterogeneity of dead wood and soil resources are also altered as canopy trees are blown over and up-rooted (Carlton and Bazzaz, 1998; Elliott et al., 2002; Palmer et al., 2000; Ulanova, 2000). In turn, these changes result in high variability of microhabitat conditions, which include fine-scale patterning of light, temperature, soil water, and soil nutrients. By changing the spatial pattern of these resources, severe wind disturbances are known to significantly alter the successional dynamics of forests over the long-term, but outcomes are inconsistent and difficult to predict given the milieu of contributing factors (Everham and Brokaw, 1996; Peterson, 2000). Foster and Orwig (2006) suggest that wind-salvaged areas may experience more dramatic alteration of forest structure, soil resources, and biogeochemical processes than windthrown areas alone. Salvage logging further has the potential to diminish the fine-scale environmental variability created by wind disturbance as downed trees are removed, existing tree seedlings and/or saplings are damaged, and soil resources are compacted and disturbed. Because of the additive effects of compound disturbances (Paine et al., 1998), windthrown areas that are also salvage logged may not be able to recover within the same timeframe as their non-salvaged counterparts.

In 1977, a severe wind event composed of 25 separate downbursts with winds reaching 253 km/h removed most of the overstory on 344,000 ha of forest in northern Wisconsin, USA. Dunn et al. (1983) document immediate changes in the composition and structure of an old-growth hemlock-northern hardwoods forest within this area. Expanding on their effort, we evaluated the long-term forest response to windthrow and salvage logging. We expected to find that the combined disturbances of windthrow and salvage logging to substantially set back succession and alter (1) forest composition and structure, (2) microrelief and soil characteristics, and (3) relationships between the understory herb community and microrelief in comparison to forests only disturbed by windthrow (Palmer et al., 2000; Ulanova, 2000; Foster and Orwig, 2006; Lindenmayer and Noss, 2006). Specifically, we expected the salvaged areas to have a higher proportion of early successional species represented in all layers of the forest, a less well-developed forest canopy, less microtopographic variation, more compact soils, and less pronounced relationships between the understory herbs community and microrelief.

In their review, Lindenmayer and Noss (2006) observe that most studies assessing the effects of salvage logging are substantially limited by their sampling frameworks. Our study overcomes most common limitations in that predisturbance and early post-disturbance data are available (Anderson and Loucks, 1979; Dunn et al., 1983), salvaged and unsalvaged areas were both affected by the same natural disturbance event, and salvaged and unsalvaged areas are located proximal to one another. A further advantage of this work is that it spans 25 years, providing the longest term data set known to us of all non-retrospective salvage logging studies we found.

2. Methods

2.1. Study area

The study area lies within the Flambeau River State Forest in Sawyer County, Wisconsin, USA (90°45′W, 45°44′N). This forest is located within the Laurentian Mixed Forest Providence, characterized by a humid-continental climate having mild summers and cold winters (Cleland et al., 2007). Key surficial geologic strata within this area include loess, outwash, and eolian sands (USDA NRCS, 2006). Soils are naturally acidic, with textures that are sandy or silty, and are nearly identical in the top 20+ cm.

Study plots were located in an area known as the "Big Block" – a 1200 ha tract of virgin, old-growth hemlock-northern hardwoods forest – up until the time of the 1977 blowdown. Quantitative data on pre-disturbance forest conditions come from the Flambeau River Hemlock-Hardwood Scientific Area (Dunn et al., 1983), a ~146 ha tract within the Big Block, although forests throughout the entire Big Block were of similar character (G.R.G., personal observation). Eastern hemlock (*Tsuga canadensis*) was the dominant overstory tree species, while yellow birch (*Betula alleghaniensis*) and sugar maple (*Acer saccharum*) were present in the subcanopy (Dunn et al., 1983). White pine (*Pinus strobus*), American elm (*Ulmus americana*), and American basswood (*Tilia americana*) were also present, but were not as common as the above species (Dunn et al., 1983). Canopy tree ages ranged from 250 to 400 years and the mean basal area within the Scientific Area was estimated to be about 41 m^2/ha. Although not allowed within the Scientific Area, adjacent forest within the Big Block was salvaged logged using conventional methods (i.e., logs were skidded across bare ground and collected on landings) in the year following the blowdown and completed within 2 years of the wind event. Directly following the disturbances, white-tailed deer (*Odecoileus virginianus*) were frequently observed in the salvaged area but never in the Scientific Area due to the large number of downed stems.

2.2. Field methods

In 1979, Dunn et al. (1983) established two sampling transects with 28 plots total within the Scientific Area, hereafter referred to as the "unsalvaged area." Although the data have not been published, 15 plots were also established along transects in nearby (<0.5 km away) areas that were salvage logged during the spring and summer of 1979. Trees were delimbed in the woods and skidded to landings by a tractor. Sampling in both salvaged and unsalvaged areas was conducted in 1979, 1990, and 2004. Each plot consisted of a 0.025 ha (10 m × 25 m) sampling area for trees, in which species and diameter at breast height (dbh) of all trees measuring ≥10 cm dbh was recorded. Saplings, shrubs, herbs, and tree seedlings were inventoried in subplots nested within the tree plot. Subplot dimensions were 0.0125 ha (5 m × 5 m), 0.0025 ha (2.5 m × 25 m), and 0.00025 ha (1 m × 2.5 m) for saplings, shrubs, and herbs/seedlings, respectively. Saplings and shrubs were counted and recorded to species while herb and seedling data were tallied as percent cover by species.

In 2004, we also randomly selected four tree tip-ups within each survey plot and measured mound height, pit depth, understory herb cover, and we gathered soil samples to a depth of 15 cm (a 188.4 cm^3 sample). Percent cover of understory herbs were tallied to species where possible in a 25-cm by 50-cm quadrat at five tip-up positions: (1) mound top, (2) mound slope, (3) pit, (4) opposite slope, and (5) a 'control' position located 2-m away from the mound on the side of the downed tree. We gathered soil samples at each of the five tip-up positions and used standard protocol to analyze them for pH, bulk density, organic carbon content, and organic nitrogen content. Organic carbon and nitrogen content are expressed as a percent weight of a 2-g sample.

2.3. Data analysis

Forest composition and structure: We used repeated measures analysis of variance (ANOVA) within SAS (SAS Institute, 1998;

PROC MIXED) to test for differences in forest recovery between salvaged and unsalvaged areas and over time. We used this model to test for differences in total tree basal area, sapling density, shrub layer density, and seedling cover.

Tip-up structure and substrate characteristics: We used micro-topographical and soil attribute data to evaluate the effect of salvage logging on tip-up structure and substrate characteristics as of 2004. Using ANOVA within SAS (PROC MIXED), we evaluated tip-up mound height, tip-up pit depth, soil bulk density, soil pH, percent organic carbon, percent organic nitrogen, and carbon:nitrogen (hereafter C:N). In evaluating the substrate characteristics of tip-ups, disturbance was treated as a fixed effect, while position within the tip-up and the interaction between position and disturbance were treated as random effects.

Understory composition and relationships with microrelief: We used two tests to compare understory herb communities within salvaged and unsalvaged areas as of 2004. We first used the multiresponse permutation procedure (MRPP), a non-parametric technique that tests the null hypothesis of no differences between predefined groups (McCune and Grace, 2002), with data on understory species frequency. We performed MRPP in PC-ORD (McCune and Mefford, 1999) with the Bray-Curtis distance measure, a robust measure for ecological community data (McCune and Grace, 2002). The presence of understory herbs was summed at the survey plot level (i.e., all samples of the herb communities within plots were combined) to compute species frequencies. Secondly, we used an ANOVA within SAS (PROC MIXED) to test for differences in species richness, total cover, and cover of individual species by disturbance type and tip-up position. Understory herbs found >2.5% more often in one disturbance type over another were included in individual species tests. Seventeen of the 53 species or species groups (e.g., *Poa* spp., *Viola* spp.) recorded met this 2.5% cutoff, which was based on a natural break in the data. Within the mixed models, disturbance was treated as a fixed effect while tip-up position and the interaction between position and disturbance were treated as random effects.

3. Results

3.1. Disturbance and forest composition and structure

We found significant differences between the unsalvaged and salvaged areas in overstory and understory regeneration (Fig. 1). In 1979, basal area in both salvaged and unsalvaged areas was low compared to the pre-disturbance level of 41 m^2/ha (Dunn et al., 1983), though over 70 times higher within the unsalvaged area on average (Fig. 1a) due to the remaining presence of partially blown over trees that re-leafed following the wind disturbance (G.R.G., personal observation). Basal area accumulation significantly differed between the two areas in the first two sampling periods (disturbance $F_{1,41} = 4.67$, $p = 0.04$; time $F_{2,82} = 49.15$, $p < 0.01$; disturbance × time $F_{2,82} = 0.23$, $p = 0.22$), but converged by 2004 (Fig. 1a). Mean tree diameter was higher, though more variable, in the salvaged area (unsalvaged: 15.37 cm [SE 0.26]; salvaged: 17.13 cm [SE 0.44]).

Although Eastern hemlock was dominant prior to the windthrow event (Dunn et al., 1983), very few individuals survived the windthrow. In 1979, the basal area of hemlock trees was 0.94 m^2/ha in the unsalvaged area and 0.04 m^2/ha in the salvaged area. It has steadily declined over time and was not recorded in the 2004 sample (disturbance $F_{1,41} = 3.20$, $p = 0.08$; time $F_{2,82} = 3.00$, $p = 0.06$; disturbance × time $F_{2,82} = 2.51$, $p = 0.09$). By 2004, tree basal area was shared among five broad-leaf deciduous species, American elm, sugar maple, American basswood, quaking aspen (*Populus tremuloides*), and yellow birch, which together represented 88% and 82% of the basal area in unsalvaged and salvaged areas, respectively. Sugar maple (disturbance $F_{1,41} = 1.87$, $p = 0.18$; time $F_{2,82} = 11.84$, $p < 0.01$; disturbance × time $F_{2,82} = 0.16$,

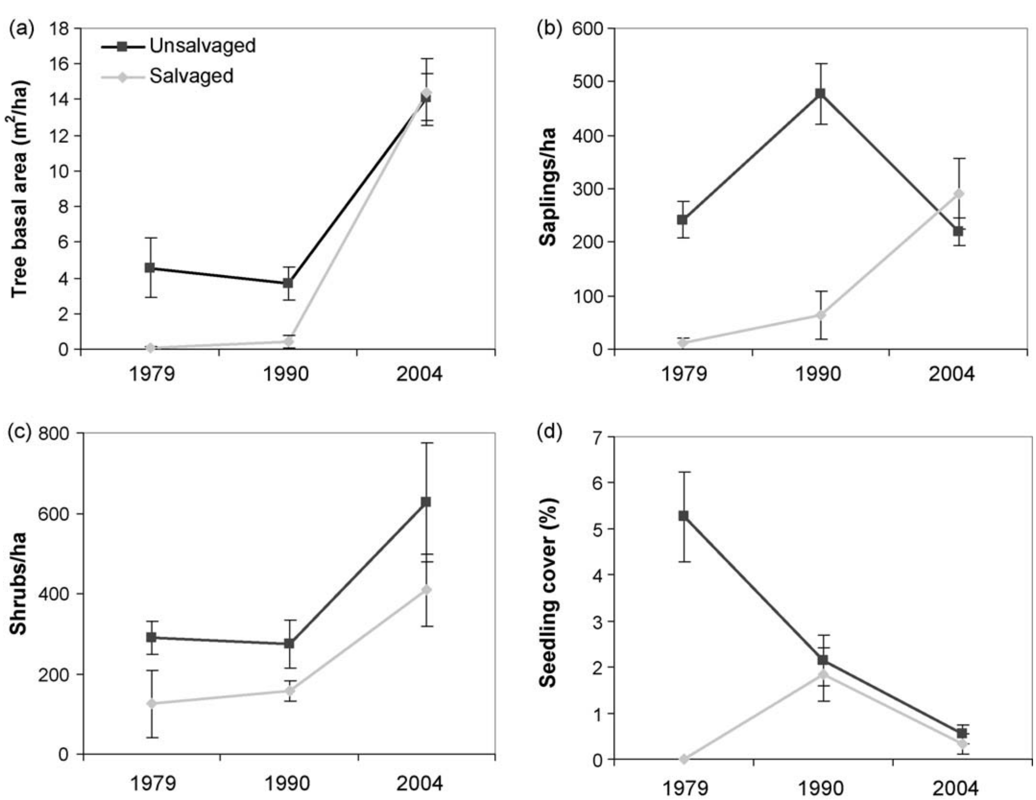

Fig. 1. Change in (a) tree basal area, (b) sapling density, (c) shrub layer density, and (d) seedling cover in unsalvaged and salvaged forests. Error bars show standard error.

$p = 0.86$), American basswood (disturbance $F_{1,41} = 3.89$, $p = 0.06$; time $F_{2,82} = 19.99$, $p < 0.01$; disturbance × time $F_{2,82} = 2.35$, $p = 0.10$), and yellow birch (disturbance $F_{1,41} = 2.57$, $p = 0.12$; time $F_{2,82} = 1.34$, $p < 0.27$; disturbance × time $F_{2,82} = 1.10$, $p = 0.34$) reached higher levels of basal area in the unsalvaged area, while American elm (disturbance $F_{1,41} = 0.11$, $p = 0.75$; time $F_{2,82} = 21.87$, $p < 0.01$; disturbance × time $F_{2,82} = 1.10$, $p = 0.33$) and quaking aspen (disturbance $F_{1,41} = 3.95$, $p = 0.05$; time $F_{2,82} = 10.16$, $p < 0.01$; disturbance × time $F_{2,82} = 3.71$, $p = 0.03$) reached higher levels in the salvaged area (Fig. 2), although the difference was only significant for aspen.

Saplings initiated prior to the disturbance (G.R.G., personal observation) were significantly more abundant in the unsalvaged than salvaged area directly following disturbance (Fig. 1b; disturbance $F_{1,41} = 25.31$, $p < 0.01$; time $F_{2,82} = 5.80$, $p < 0.01$; disturbance × time $F_{2,82} = 13.82$, $p < 0.01$). Sapling densities spiked in the unsalvaged area around 1990, and then fell below initial post-disturbance levels (Fig. 1b); this pattern was common to all dominant sapling species: sugar maple, American basswood, yellow birch, and American elm. Sapling densities in the salvaged area, in contrast, showed near linear increases over time (Fig. 1b), due predominantly to increases in American elm, but also sugar maple. The pattern of the shrub layer development also differed between unsalvaged and salvaged areas over time (Fig. 1c; disturbance $F_{1,41} = 4.25$, $p = 0.05$; time $F_{2,82} = 6.31$, $p < 0.01$; disturbance × time $F_{2,82} = 0.13$, $p = 0.88$).

Seedlings were recorded in the unsalvaged area and not in the salvaged area directly following disturbance (Fig. 1d). Although tree seedling cover has remained low in both areas over time, it does differ significantly (disturbance $F_{1,41} = 12.17$, $p = 0 < 0.01$; time $F_{2,82} = 5.59$, $p < 0.01$; disturbance × time $F_{2,82} = 9.18$, $p < 0.01$). In 1979, seedling species most commonly recorded in the unsalvaged area included sugar maple, yellow birch, and American basswood. By 2004, white ash (*Fraxinus americana*) seedlings were found on 21% of the study plots in the unsalvaged area; red maple (*A. rubrum*) and black cherry (*Prunus serotina*) Mohr seedlings were each found on one plot in the salvaged area.

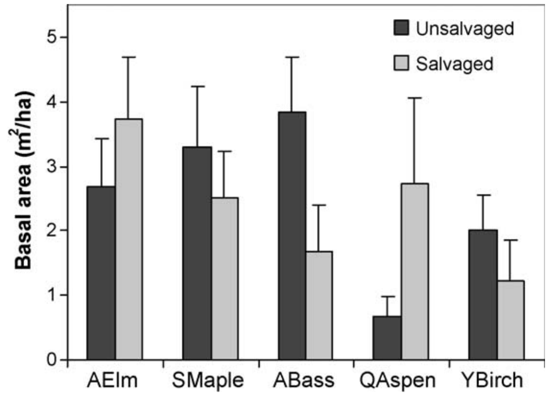

Fig. 2. Basal area of dominant tree species in unsalvaged and salvaged forests in 2004. AElm = American elm (*Ulmus americana*); SMaple = sugar maple (*Acer saccharum*); ABass = American basswood (*Tilia americana*); QAspen = quaking aspen (*Populus tremuloides*); and YBirch = yellow birch (*Betula alleghaniensis*). Error bars show standard error.

3.2. Disturbance and tip-up structure and substrate characteristics

We found a significant difference in tip-up structure between the two disturbances, with significantly higher mounds ($F_{1,169} = 45.84$; $p < 0.01$) and deeper pits ($F_{1,169} = 11.44$; $p < 0.01$) in the unsalvaged area. Average mound height was 0.62 m (SE 0.03) and pit depth was 0.24 m (SE 0.01) in the unsalvaged area. In the salvaged area, mound height was 0.35 m (SE 0.02) and pit depth was 0.15 m (SE 0.02).

In evaluating tip-up substrate characteristics, we found significant differences both by disturbance and position for soil bulk density, organic carbon content, and organic nitrogen content (Table 1). Bulk density averaged 0.10 g/cm^3 higher within the salvaged area, was highest in mound side and opposite side positions, and lowest in pit and control positions. Mean soil organic carbon and nitrogen were, respectively, 1.91% and 0.19% higher within the salvaged area. Both attributes were highest in pit and

Table 1
Response of soil attributes to disturbance type, tip-up position, and their interaction.

Soil attribute	Position	Unsalvaged	Salvaged	Disturbance		Position		Interaction	
		Mean (SE)	Mean (SE)	$F_{1,845}$	p	$F_{4,845}$	p	$F_{4,845}$	p
Bulk density (g/cm^3)	Top	1.81 (0.05)	1.98 (0.06)	6.03	0.01	9.06	<0.01	1.34	0.25
	Mound side	2.07 (0.05)	2.01 (0.05)						
	Pit	1.68 (0.06)	1.77 (0.08)						
	Opposite side	1.91 (0.06)	1.99 (0.06)						
	Control	1.66 (0.05)	1.86 (0.06)						
pH	Top	4.67 (0.04)	4.70 (0.07)	7.41	<0.01	1.97	0.1	0.26	0.91
	Mound side	4.60 (0.04)	4.69 (0.05)						
	Pit	4.70 (0.04)	4.84 (0.06)						
	Opposite side	4.70 (0.06)	4.82 (0.06)						
	Control	4.71 (0.05)	4.82 (0.08)						
Organic carbon content (%)	Top	3.03 (0.25)	4.98 (0.75)	37.13	<0.01	10.51	<0.01	1.02	0.4
	Mound side	2.15 (0.15)	4.31 (0.29)						
	Pit	4.49 (0.47)	7.42 (0.80)						
	Opposite side	3.83 (0.48)	5.29 (0.48)						
	Control	5.13 (0.46)	6.20 (0.70)						
Organic nitrogen content (%)	Top	0.22 (0.02)	0.40 (0.05)	112.4	<0.01	14.74	<0.01	1.25	0.29
	Mound side	0.17 (0.01)	0.37 (0.02)						
	Pit	0.32 (0.02)	0.57 (0.05)						
	Opposite side	0.27 (0.02)	0.42 (0.03)						
	Control	0.36 (0.02)	0.50 (0.05)						
C:N	Top	13.15 (0.29)	11.62 (0.23)	35.86	<0.01	1.12	0.35	0.2	0.94
	Mound side	12.70 (0.25)	11.57 (0.26)						
	Pit	13.21 (0.26)	12.19 (0.28)						
	Opposite side	12.84 (0.39)	11.68 (0.37)						
	Control	13.35 (0.29)	11.95 (0.28)						

control positions, and lowest on mound sides. pH and C:N differed by disturbance, but not for position (Table 1). pH was consistently higher within the salvaged area and C:N within the unsalvaged area. With the exception of organic nitrogen content (unsalvaged = 1.72%; salvaged = 2.25%), soil attributes showed a greater level of variation in the unsalvaged (data range for bulk density = 3.27 g/cm^3; pH 6.4; organic carbon = 46.81%; C:N = 46.03) compared to the salvaged area (data range for bulk density = 2.86 g/cm^3; pH 3.4; organic carbon = 37.75%; C:N = 20.61).

3.3. Disturbance, tip-up structure, and understory response

Overall community composition, as determined by MRPP, differed between salvaged and unsalvaged areas ($T \approx -4.27$; $A \approx 0.02$; $p < 0.01$). The average Bray-Curtis distance between understory herb community samples within the salvaged area was 0.5562; the average Bray-Curtis distance among samples from the unsalvaged area was 0.5817. Species richness differed by disturbance type ($F = 14.86$, $p < 0.01$) and tip-up position ($F = 22.86$, $p < 0.01$; Fig. 3a); the interaction between disturbance and position was not significant ($F = 0.62$, $p = 0.65$). Species richness was higher in the salvaged area (mean = 5.76 species/m^2 [SE 0.20]); unsalvaged mean = 4.88 species/m^2 [SE 0.14]; Fig. 3a). Species richness was highest on mound tops (mean = 6.48 species/m^2 [SE 0.22] and lowest in pits; mean = 3.23 species/m^2 [SE 0.21]; Fig. 3a). The species most commonly recorded were shared between the two areas and included *Poa* species (26.08% of total samples), moss species (25.15%), *Athyrium filix-femina* (24.44%), *Laportea canadensis* (16.84%), and *Hydrophyllum virginianum* (14.50%). Moss species (26.43%), *Gymnocarpium dryopteris* (10.71%), and *Dryopteris* species (10.28%) were recorded more frequently in the unsalvaged area, while *Poa* species (36.95%), *A. filix-femina* (30.85%), *H. virginianum* (20.34%), *L. canadensis* (19.32%), *Solidago* species (14.24%), and *Viola* species (12.88%) were recorded more frequently in the salvaged area. The overall incidence of tree seedlings on tip-up plots was low, but was more frequent in the unsalvaged (8.21%) – where *B. alleghaniensis* was most commonly recorded species (1.96%) – than the salvaged area (5.07%). We recorded bare ground twice as frequently in the unsalvaged (11.61%) as the salvaged area (6.10%).

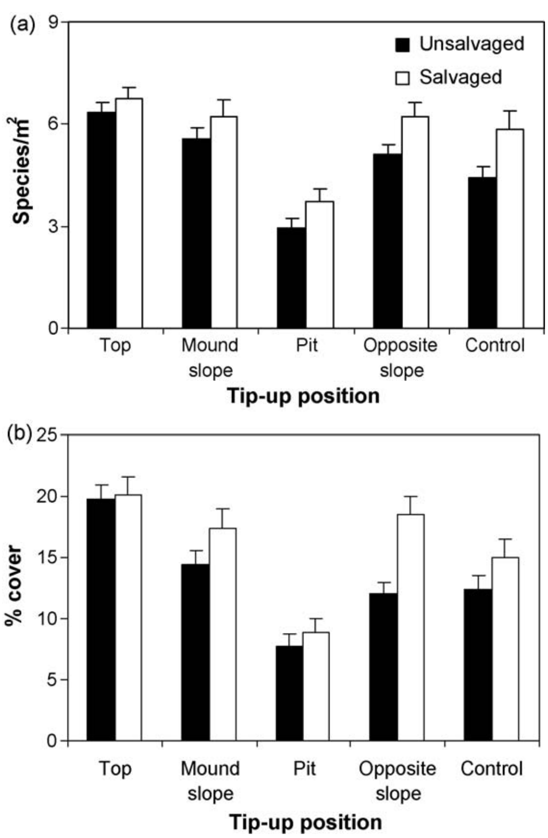

Fig. 3. Understory herb (a) richness and (b) cover by tip-up position in unsalvaged and salvaged forests. Error bars show standard error.

Patterns in forest herb cover mimicked those of species richness and differed by disturbance type ($F = 11.46$, $p < 0.01$; Fig. 3b) and tip-up position ($F = 22.46$, $p < 0.01$); the interaction between the two was not significant ($F = 1.71$, $p = 0.15$). Cover was higher within the salvaged area (mean = 15.97% [SE 0.68]; unsalvaged mean = 13.27% [SE 0.49]), and was highest on mound tops (19.88% [SE 0.88]) and lowest in pits (mean = 8.12% [SE 0.75]; Fig. 3b).

Our mixed models revealed distinct patterns in species response to disturbance type and tip-up position (Table 2). *Dryopteris* species, *Fragaria* species, *Osmorhiza claytonii*, *Solidago* species, *Viola* species, and *Uvularia grandiflora* responded to disturbance type, but not to tip-up position; *Dryopteris*, *Fragaria* species, and *U. grandiflora* cover were higher in the unsalvaged area, while *O. claytonia*, *Solidago* and *Viola* species cover was higher in the salvaged area (Table 2). *A. filix-femina*, *Maianthemum canadense*, moss species, *Poa* species, and *Trientalis borealis* responded to both disturbance type and tip-up position (Table 2), and all four reach higher percent covers in the salvaged area. *M. canadense*, *Poa* species, and *T. borealis* cover was highest on mound tops and lowest in pits in both disturbance types. The response of *A. filix-femina* to microrelief was more complex, and varied by disturbance type. Moss cover was highest on mound tops in the unsalvaged area. *G. dryopteris*, *H. virginianum*, and *Polygonum cilinode* responded in various ways to tip-up position, but not disturbance type: *G. dryopteris* cover was highest on mound tops, *H. virginianum* cover was lowest on mound tops, and *P. cilinode* was lowest in pits across disturbances (Table 2). The interaction between disturbance and tip-up position was significant only for moss cover and *U. grandiflora*, though *A. pedatum* trended toward significance (Table 2). *L. canadensis* and *Polygonatum biflorum* did not respond to either disturbance type or tip-up position (Table 2). While *L. canadensis* was commonly recorded, especially in the salvaged area, *P. biflorum* was always found at low frequencies and levels of cover.

4. Discussion

4.1. Overstory recovery following windthrow and salvage logging

At 25 years following windthrow and salvage logging, our work supports others' in showing that salvage logging alters the successional dynamics of naturally disturbed forest (Foster et al., 1997; Cooper-Ellis et al., 1999; van Nieuwstadt et al., 2001; Lindenmayer and Ough, 2006), though the alteration we found is not as dramatic as these other studies would suggest. Biological legacies, including seedlings, saplings, and mature trees that survived the disturbance, were significantly more abundant in the unsalvaged area soon after disturbance (Fig. 1a and b); many of the trees currently comprising the canopy were present in the understory at the time of windthrow. The disturbance event promoted seed germination and seedling establishment (Fig. 1d), primarily in sugar maple, yellow birch, and American basswood. Yellow birch is known to be a prolific seeder following windthrow (Burns and Honkala, 1990), and its persistence in the region may be linked to severe windthrow events as experienced on the Flambeau in 1977 (Schulte and Mladenoff, 2005). Two legacies of windthrow – downed tree boles and tree tip-ups – are known to provide conditions important to the successful seed germination and establishment of yellow birch as well as other tree and herb

Table 2
Understory herb and moss response, as measured by percent cover, to disturbance type, tip-up position, and their interaction.

Species	Position	Unsalvaged	Salvaged	Disturbance		Position		Interaction	
		Mean (SE)	Mean (SE)	$F_{1,845}$	p	$F_{4,845}$	p	$F_{4,845}$	p
Adiantum pedatum	Top	0.31 (0.18)	0 (0)	0.01	0.93	1.49	0.2	2.26	0.06
	Mound Side	0.60 (0.22)	0.17 (0.13)						
	Pit	0.38 (0.19)	0.42 (0.32)						
	Opposite Side	0.20 (0.10)	1.06 (0.71)						
	Control	0.22 (0.12)	0 (0)						
Athyrium filix- femina	Top	0.85 (0.28)	2.92 (0.90)	9.81	<0.01	2.33	0.05	1.86	0.12
	Mound Side	1.29 (0.32)	3.52 (0.83)						
	Pit	1.45 (0.29)	1.82 (0.72)						
	Opposite Side	2.39 (0.51)	3.05 (0.82)						
	Control	1.32 (0.43)	1.27 (0.41)						
Dryopteris spp.	Top	0.33 (0.12)	0.13 (0.13)	18.54	<0.01	0.87	0.48	0.6	0.66
	Mound Side	0.40 (0.10)	0.04 (0.04)						
	Pit	0.20 (0.06)	0 (0)						
	Opposite Side	0.45 (0.11)	0 (0)						
	Control	0.20 (0.10)	0 (0)						
Fragaria spp.	Top	0.22 (0.22)	0 (0)	6.47	0.01	0.51	0.73	0.51	0.73
	Mound Side	0.16 (0.16)	0 (0)						
	Pit	0.07 (0.07)	0 (0)						
	Opposite Side	0.04 (0.04)	0 (0)						
	Control	0.09 (0.09)	0 (0)						
Gymnocarpium dryopteris	Top	0.74 (0.25)	1.23 (0.71)	0.1	0.75	3.46	<0.01	0.85	0.49
	Mound Side	0.49 (0.18)	0.47 (0.22)						
	Pit	0.18 (0.08)	0.04 (0.04)						
	Opposite Side	0.47 (0.18)	0.17 (0.13)						
	Control	0.49 (0.15)	0.21 (0.14)						
Hydrophyllum virginianum	Top	0.29 (0.18)	0.42 (0.19)	1.07	0.3	2.52	0.04	1.47	0.21
	Mound Side	0.69 (0.22)	0.89 (0.37)						
	Pit	1.96 (0.80)	1.02 (0.44)						
	Opposite Side	1.16 (0.33)	2.42 (0.91)						
	Control	0.76 (0.36)	1.78 (0.44)						
Laportea canadensis	Top	0.54 (0.19)	1.36 (0.42)	3.01	0.08	0.84	0.5	1.17	0.32
	Mound Side	0.65 (0.22)	0.72 (0.26)						
	Pit	0.65 (0.18)	1.02 (0.37)						
	Opposite Side	0.96 (0.23)	0.68 (0.23)						
	Control	0.89 (0.27)	1.44 (0.42)						
Maianthemum canadense	Top	0.25 (0.09)	0.59 (0.20)	7.06	<0.01	5.93	<0.01	1.52	0.19
	Mound Side	0.20 (0.08)	0.17 (0.08)						
	Pit	0.02 (0.02)	0.08 (0.06)						
	Opposite Side	0.02 (0.02)	0.13 (0.07)						
	Control	0.02 (0.02)	0.25 (0.14)						
Moss spp.	Top	7.57 (1.09)	1.95 (0.44)	8.57	<0.01	16.52	<0.01	6.67	<0.01
	Mound Side	3.71 (0.86)	2.63 (0.79)						
	Pit	0.20 (0.10)	0.42 (0.19)						
	Opposite Side	0.25 (0.09)	0.97 (0.26)						
	Control	0.87 (0.57)	0.21 (0.09)						
Osmorhiza claytonii	Top	0.09 (0.07)	0.13 (0.07)	3.77	0.05	1.42	0.23	1.38	0.24
	Mound Side	0.07 (0.04)	0 (0)						
	Pit	0 (0)	0.34 (0.30)						
	Opposite Side	0.25 (0.10)	0.30 (0.18)						
	Control	0.02 (0.02)	0.30 (0.11)						
Poa spp.	Top	1.83 (0.33)	3.35 (0.82)	30.55	<0.01	15.29	<0.01	2.09	0.08
	Mound Side	0.76 (0.15)	1.40 (0.29)						
	Pit	0.16 (0.06)	0.34 (0.11)						
	Opposite Side	0.51 (0.14)	1.91 (0.44)						
	Control	0.36 (0.10)	1.95 (0.48)						
Polygonatum biflorum	Top	0 (0)	0.04 (0.04)	1.5	0.22	2.12	0.08	0.52	0.72
	Mound Side	0.07 (0.04)	0.08 (0.06)						
	Pit	0.04 (0.03)	0.13 (0.07)						
	Opposite Side	0.07 (0.04)	0.30 (0.15)						
	Control	0.27 (0.17)	0.25 (0.10)						
Polygonum cilinode	Top	0.25 (0.09)	0.34 (0.19)	0.95	0.33	2.78	0.03	1.21	0.31
	Mound Side	0.18 (0.08)	0.25 (0.14)						
	Pit	0.07 (0.04)	0 (0)						
	Opposite Side	0.16 (0.08)	0 (0)						
	Control	0.22 (0.07)	0 (0)						

Table 2 (*Continued*)

Species	Position	Unsalvaged	Salvaged	Disturbance		Position		Interaction	
		Mean (SE)	Mean (SE)	$F_{1,845}$	p	$F_{4,845}$	p	$F_{4,845}$	p
Solidago spp.	Top	0.20 (0.08)	1.86 (0.91)	18.8	<0.01	0.98	0.42	0.44	0.78
	Mound Side	0.78 (0.57)	2.08 (0.94)						
	Pit	0.11 (0.05)	0.76 (0.42)						
	Opposite Side	0.31 (0.12)	1.74 (0.93)						
	Control	0.04 (0.03)	1.95 (0.93)						
Trientalis borealis	Top	0.11 (0.07)	0.42 (0.19)	9.03	<0.01	4.63	<0.01	1.35	0.25
	Mound Side	0.02 (0.02)	0.08 (0.06)						
	Pit	0 (0)	0.04 (0.04)						
	Opposite Side	0 (0)	0.08 (0.06)						
	Control	0 (0)	0.13 (0.13)						
Uvularia grandiflora	Top	0 (0)	0.13 (0.13)	4.87	0.03	1.52	0.19	3.05	0.02
	Mound Side	0.11 (0.07)	0.17 (0.13)						
	Pit	0.09 (0.04)	0.04 (0.04)						
	Opposite Side	0.45 (0.19)	0 (0)						
	Control	0.78 (0.27)	0 (0)						
Viola spp.	Top	0.22 (0.09)	0.38 (0.16)	15.45	<0.01	0.51	0.73	0.35	0.84
	Mound Side	0.20 (0.10)	0.38 (0.12)						
	Pit	0.04 (0.03)	0.34 (0.11)						
	Opposite Side	0.16 (0.06)	0.51 (0.20)						
	Control	0.09 (0.04)	0.42 (0.19)						

species (Beatty, 1984; Carlton and Bazzaz, 1998; Palmer et al., 2000; Ulanova, 2000; Marx and Walters, 2006). Similar to other studies (van Nieuwstadt et al., 2001; Donato et al., 2006), we found no seedlings and few trees and saplings that survived salvage logging (Fig. 1a, b and d). Rather, canopy trees in this area today largely sprouted from the roots or stumps of cut trees, and thus are also biological legacies of the pre-disturbance forest. Biological legacies generally refer to the number and spatial arrangements of downed trees and snags left by the natural disturbance (Lindenmayer et al., 2004). We have expanded "legacies" to include the stumps and roots left from the cut trees as they still serve an important role in the salvaged area even though the main portion of the tree was harvested. All of the now dominant tree species in the salvaged area have the ability to vigorously root sucker or stump sprout (Burns and Honkala, 1990). Despite the loss of most pre-disturbance seedlings, saplings, and trees from windthrow and salvage logging, recovery was not set back much further in this forest than forest disturbed by windthrow alone. As of 2004, the unsalvaged and salvaged areas shared dominant species (Fig. 2) and had converged in terms of tree basal area, sapling density, shrub layer density, and seedling cover (Fig. 1). The only factor in support of our hypothesis that combined disturbances would set back succession further than windthrow alone was the higher basal area of quaking aspen (an early invader of disturbed areas) in the salvaged forest.

In neither case do the disturbed forests show signs of hemlock recovery, a conservation concern given the widespread loss of this foundational species in the region (Ellison et al., 2005; Schulte et al., 2007). Anderson and Loucks (1979) recognize that the reproductive success of Eastern hemlock had diminished on the Flambeau even prior to windthrow and salvage logging. Several factors influenced the decline of hemlock in the region including competition from rapidly regenerating broad-leaf deciduous species, an increase in deer browsing levels, and climate change (Mladenoff and Stearns, 1993; Rooney et al., 2000). It is improbable that salvage logging contributed to hemlock's decline.

4.2. Salvage logging effects on microtopography and soil

Pit-and-mound microtopography formed through windthrow increases the structural complexity of the forest floor by disrupting soil horizons, exposing organic and mineral soil, creating gradients of soil water content, generating small-scale temperature differences, and altering soil development (Beatty, 1984; Ulanova, 2000). Lasting up to 500 years after formation (Tyrrell and Crow, 1994), tip-up microtopography forms a structural legacy in windthrown forests important to the regeneration of some tree and understory species (Carlton and Bazzaz, 1998; Palmer et al., 2000; Ulanova, 2000). As we expected, salvage logging diminished these legacies of windthrow in our forest. While tip-up mounds naturally wear down over time through erosional processes and pits fill with sediment and debris (Beatty, 1984; Ulanova, 2000), salvage practices augment this leveling by further exposing, moving, and compressing soil during harvest. In common with other salvage logging studies (Beschta et al., 2004; Lindenmayer and Noss, 2006; Peterson and Leach, 2008a), we also recorded higher levels of soil bulk density – hence, compaction – both on and off tree tip-ups in the salvaged area (Table 1).

Yet, the effects of salvage logging on soil are not limited to structure (Foster and Orwig, 2006; Rumbaitis del Rio, 2006). Although we found higher organic nitrogen content, organic carbon content, and pH in the soils of salvaged forest (Table 1), the more salient effect of salvage logging may be the homogenization of soil resources. Higher variability in these measures and the higher incidence of bare ground that we recorded in unsalvaged forest suggest fine-scale spatial patterns that may be important in maintaining forest understory biodiversity.

4.3. Salvage logging effects on understory response to microtopography

Our analysis reveals strong patterns in understory herb and moss response to forest microtopography (Table 2; Fig. 3), with species richness and cover highest on mound tops and lowest in pits, supporting the findings of previous studies (Beatty, 1984; Carlton and Bazzaz, 1998; Palmer et al., 2000; Ulanova, 2000). This pattern is particularly noteworthy given the effects of salvage logging on microtopography. While responses to the combination of disturbance and tip-up position were variable among the species we studied, clear patterns existed in the response to disturbance alone (Table 2).

We recorded higher levels of both understory cover and species richness in salvaged forest (Fig. 3). The stronger response of understory cover in the salvaged area is due to the comparatively more open canopy conditions maintained in that area for some time (Fig. 1a and b) and the additional amount mineral soil exposed during the salvage operation (G.R.G. personal observation), together favoring the establishment of disturbance-adapted species. These results are consistent with other studies of understory response to salvage logging in mesic forests of the eastern U.S. As with Elliott et al. (2002), we found (1) that the herbaceous community quickly rebounded following salvage logging of windthrown forest, (2) a mix of shade-intolerant and -tolerant forbs within salvaged forest, and (3) a mixed response among more conservative species found on our sites. Exemplifying this last point, the cover of *U. grandiflora* (coefficient of conservatism [cc] = 7; WSH, 2008) was higher within the unsalvaged area, *T. borealis* (cc = 7) was higher in the salvaged area, and *A. pedatum* (cc = 7) and *G. dryopteris* (cc = 7) did not differ by disturbance type. The value of 7 for the coefficient of conservatism suggests plants with a poor range of ecological tolerance associated with advanced successional state (WSH, 2008). Peterson and Leach (2008b) report similar response among understory herbaceous and tree seedling communities in salvaged and unsalvaged windthrown forest. Drier western forests may provide a contrast (Rumbaitis del Rio, 2006).

Although we record higher mean species richness within the salvaged area, much of the difference is due to substantially higher frequencies of a few species common to both areas, including *A. filix-femina*, *H. virginianum*, *L. canadensis*, and species in the genera *Poa*, *Solidago*, and *Viola*. Extending the results of other studies of logging disturbance in the region, which show that increases in understory richness and cover are primarily due to the response of already common species (Crow et al., 2002; Wolf et al., 2008), we suggest that the impact of the combined disturbances of windthrow and logging on understory communities may not be very different than the impact of logging alone. Although undisturbed controls were not present in our study, others report much higher levels of plant community diversity in windthrown forest in comparison to adjacent, undisturbed forest (Palmer et al., 2000; Cooper-Ellis et al., 1999; Elliott et al., 2002; Rumbaitis del Rio, 2006).

5. Conclusions

At 25 years following severe windthrow on and nearby the Flambeau Scientific and Natural Area, Wisconsin, unsalvaged and salvage logged forests had converged in terms of composition and structure, but bore little resemblance to their pre-disturbance state. Although recovery pathways differed, biological legacies from the previous forest were important to forest regrowth in *both* cases. While the biological legacies of pre-disturbance seedlings, saplings, and trees were removed with salvage logging, forest regeneration still preceded quickly via new root suckers, stump sprouts, and seedlings. By vegetative measures of forest recovery, this forest appears to be resilient to the combined disturbances of windthrow and salvage logging. Merging these results with those of two other recent studies from mesic forests of the eastern U.S. (Elliott et al., 2002; Peterson and Leach, 2008a) suggests an overall different pattern of response to salvage logging than to that reported from fire-salvaged areas (van Nieuwstadt et al., 2001; Donato et al., 2006; Lindenmayer and Ough, 2006).

We also found that unsalvaged and salvaged forests differed in the remaining *structural* legacies, including microtopographic variation associated with tree tip-ups, soil bulk density, and soil substrate characteristics. It is well known that the removal or alteration of such attributes can have long-term effects (Cooper-Ellis et al., 1999; Lindenmayer and Noss, 2006). On the Flambeau, these features may have contributed to a different pathway of forest regeneration in the case of a less severe wind disturbance—one that included recapture of the site by Eastern hemlock. Tree tip-ups comprise critical regeneration sites for hemlock in the region because they are often characterized by exposed mineral soils (Krueger and Peterson, 2006). Given that so few mature hemlocks survived the initial windthrow, however, such a potential was never tested. A more formidable conservation issue for these forests is their apparent lack of resilience to the combination of decades of intensive deer browse followed by severe windthrow. Compositional differences in the understory, especially in response to microtopographic variation, may be indicative of future divergence between unsalvaged and salvaged areas and highlight the importance of tree tip-ups in maintaining biodiversity within the herbaceous understory community.

Acknowledgments

Funding for this project was provided by the U.S. Federal McIntire-Stennis Funds, Iowa State University, and the U.S. Geological Survey. G.R. Guntenspergen also acknowledges the support of a Sigma Xi Grant-In-Aid of Research that initiated this study in 1979 and support from the National Geographic Society and the American Philosophical Society to continue the long-term monitoring at this site. We thank T. Anderson for assistance in the field work, M.J. Burkgren for soil sample preparation, L. Burras for assistance with and advice on soil analysis, C. Mabry McMullen for assistance in analyzing understory herb data, P. Caragea for statistical advice, and R. Atwell and especially C. Peterson for comments on the manuscript. C.P. Dunn and J. Dorney were instrumental in helping to establish permanent plots in 1979.

References

Anderson, R.C., Loucks, O.L., 1979. White-tailed deer (*Odecoileus virginianus*) influence on the structure and composition of *Tsuga canadensis* forests. Journal of Applied Ecology 16, 855–861.
Batista, W.B., Platt, W.J., 2003. Tree population responses to hurricane disturbance: syndromes in the south-eastern USA old-growth forest. Journal of Ecology 91, 197–212.
Beatty, S.W., 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. Ecology 65, 1406–1419.
Beschta, R.L., Rhodes, J.J., Kauffman, J.B., Gresswell, R.E., Minshall, F.W., Karr, J.R., Perry, D.A., Hauer, F.R., Frissell, C.A., 2004. Postfire management on forested public lands of the western United States. Conservation Biology 18, 957–967.
Boose, E.R., Serrano, M.I., Foster, D.R., 2004. Landscape and regional impacts of hurricanes in Puerto Rico. Ecological Monographs 74 335–352, 701 pages.
Burns, R.M., Honkala, B.H., 1990. Silvics of North America Volume 2: Hardwoods. Agricultural Handbook, vol. 654. USDA Forest Service, Washington, DC Available from http://www.na.fs.fed.us/spfo/pubs/silvics_manual/table of contents.htm (accessed September 2009), 877 pp.
Carlton, G.C., Bazzaz, E.A., 1998. Regeneration of three sympatric birch species on experimental hurricane blowdown microsites. Ecological Monographs 68 99–120, 594 pp.
Cleland, D.T., Freeouf, J.A., Keys, Jr, J.E., Nowacki, G.J., Carpenter, C., McNab, W.H., 2007. Ecological Subregions: Sections and Subsections of the Conterminous United States [1:3,500,000] [CD-ROM]. Gen. Tech. Report WO-76. U.S. Department of Agriculture Forest Service, Washington, DC.
Cooper-Ellis, S., Foster, D.R., Carlton, F., Lezberg, A., 1999. Forest response to catastrophic wind: results from an experimental hurricane. Ecology 80, 2683–2696.
Crow, T.R., Buckley, D.S., Nauertz, E.A., Zasada, J.C., 2002. Effects of management on the composition and structure of northern hardwood forests in Upper Michigan. Forest Science 48, 129–145.
Donato, D.C., Fontaine, J.B., Campbell, J.L., Robinson, W.D., Kauffman, J.B., Law, B.E., 2006. Post wildfire logging hinders regeneration and increases fire risk. Science 311, 352.
Dunn, C.P., Guntenspergen, G.R., Dorney, J.R., 1983. Catastrophic wind disturbance in an old-growth hemlock-hardwood forest, Wisconsin. Canadian Journal of Botany 61, 211–217.
Elliott, K.J., Hitchcock, S.L., Kruger, L., 2002. Vegetation response to large scale disturbance in a southern Appalachian forest: Hurricane Opal and salvage logging. Journal of the Torrey Botanical Society 129, 48–59.
Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliot, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von Holle, B., Webster, J.R., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 9, 479–486.

Everham III, E.M., Brokaw, N.V., 1996. Forest damage and recovery from catastrophic wind. Botanical Review 62, 114–185.
Fischer, A., Lindner, M., Abs, C., Lasch, P., 2002. Vegetation dynamics in central European forest ecosystems (near-natural as well as managed) after storm events. Folia Geobotanica 37, 17–32.
Foster, D.R., Aber, J.D., Melillo, J.M., Bowden, R.D., Bazzaz, F.A., 1997. Forest response to disturbance and anthropogenic stress. BioScience 47, 437–445.
Foster, D.R., Orwig, D.A., 2006. Preemptive and salvage harvesting of New England forests: when doing nothing is a viable alternative. Conservation Biology 20, 959–970.
Krueger, L.M., Peterson, C.J., 2006. Effects of white-tailed deer on *Tsuga canadensis* regeneration: evidence of microsites as refugia from browsing. American Midland Naturalist 156, 353–362.
Lindenmayer, D., Foster, D.R., Franklin, J.F., Hunter, M.L., Noss, R.F., Schmiegelow, F.A., Perry, D., 2004. Salvage harvesting policies after natural disturbance. Science 303, 1303.
Lindenmayer, D., Noss, R.F., 2006. Salvaged logging, ecosystem processes, and biodiversity conservation. Conservation Biology 20, 949–958.
Lindenmayer, D., Ough, K., 2006. Salvage logging in the montane ash eucalypt forests of the central highlands of Victoria and its potential impacts on biodiversity. Conservation Biology 20, 1005–1015.
Marx, L.M., Walters, M.B., 2006. Effects of nitrogen supply and wood species on *Tsuga canadensis* and *Betula alleghaniensis* seedling growth on decaying wood. Canadian Journal of Forest Research 36, 2873–2884.
McCune, B., Mefford, M.J., 1999. PC-ORD: Multivariate Analysis of Ecological Data, vol. 4. MjM Software Design, Gleneden Beach, Oregon, 300 pp.
McCune, B., Grace, J., 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon.
Mladenoff, D.J., Stearns, F., 1993. Eastern hemlock regeneration and deer browsing in the northern Great Lakes region: a re-examination and model simulation. Conservation Biology 7, 889–900.
Paine, R.T., Tegner, M.J., Johnson, E.A., 1998. Compound disturbances yield ecological surprises. Ecosystems 1, 535–545.
Palmer, M.W., McAlister, S.D., Arevalo, J.R., DeCoster, J.K., 2000. Changes in the understory during 14 years following catastrophic windthrow two Minnesota forests. Journal of Vegetation Science 11, 841–854.
Peterson, C.J., 2000. Catastrophic wind damage to North American forests and the potential impact of climate change. The Science of the Total Environment 262, 287–311.
Peterson, C.J., Leach, A.D., 2008a. Limited salvage logging effects on forest regeneration after moderate-severity windthrow. Ecological Applications 18, 407–420.
Peterson, C.J., Leach, A.D., 2008b. Salvage logging after windthrow alters microsite diversity, abundance and environment, but not vegetation. Forestry 81, 361–376.
Rooney, T.P., McCormick, R.J., Solheim, S.L., Waller, D.M., 2000. Regional variation in recruitment of hemlock seedlings and saplings in the upper Great Lakes USA. Ecological Applications 10, 1119–1132.
Rumbaitis del Rio, C.M., 2006. Changes in understory composition following catastrophic windthrow and salvage logging in a subalpine forest ecosystem. Canadian Journal of Forest Research 36, 2943–2954.
SAS Institute, 1998. SAS Online Doc, Version 8. SAS Institute, Ashville, North Carolina Available from http://v8doc.sas.com/sashtml (accessed September 2009).
Schulte, L.A., Mladenoff, D.J., 2005. Severe wind and fire regimes in northern Wisconsin (USA) forests: historical variability at the regional scale. Ecology 86, 431–445.
Schulte, L.A., Mladenoff, D.J., Crow, T.R., Merrick, L., Cleland, D.T., 2007. Homogenization of northern U.S. Great Lakes forests as a result of land use. Landscape Ecology 22, 1089–1103.
Sinton, D.S., Jones, J.A., Ohmann, J.L., Swanson, F.J., 2000. Windthrow disturbance, forest composition, and structure in the Bull Run basin, Oregon. Ecology 81, 2539–2556.
Tyrrell, L.E., Crow, T.R., 1994. Structural characteristics of old-growth hemlock-hardwood forests in relation to age. Ecology 75, 370–386.
Ulanova, N.G., 2000. The effects of windthrow on forests at different spatial scales: a review. Forest Ecology and Management 135, 155–167.
United States Department of Agriculture Natural Resource Conservation Service (USDA NRCS), 2006. Soil Survey for Sawyer County, Wisconsin, USA. USDA NRCS, Washington, DC Available from http://soildatamart.nrcs.usda.gov/Manuscripts/WI113/0/Sawyer_WI.pdf (accessed September 2009).
van Nieuwstadt, M.G.L., Sheil, D., Kartawinata, K., 2001. The ecological consequences of logging in the burned forests of East Kalimantan, Indonesia. Conservation Biology 15, 1183–1186.
Wisconsin State Herbarium (WSH), 2008. Wisflora: Wisconsin Vascular Plant Species. University of Wisconsin, Madison, Wisconsin Available from http://www.botany.wisc.edu/wisflora/ (accessed September 2009).
Wolf, A.T., Parker, L., Fewless, G., Corio, K., Sundance, J., Howe, R., Gentry, H., 2008. Impacts of summer versus winter logging on understory vegetation in the Chequamegon-Nicolet National Forest. Forest Ecology and Management 254, 35–45.