

Disturbance effects on herbaceous layer vegetation and soil nutrients in *Populus* forests of northern lower Michigan

Roberts, M.R.^{1*} & Gilliam, F.S.²

¹Faculty of Forestry and Environmental Management, University of New Brunswick, P.O. Box 44555, Fredericton, N.B., Canada E3B 6C2; ²Department of Biological Sciences, Marshall University, Huntington, WV 25755, USA;
*Author for correspondence; Tel. +1 506 453 4923; Fax +1 506 453 3538; E-mail ROBERTS@UNB.CA

Abstract. Recent disturbance models have identified changes in resource availability as factors that control plant community response. Soil nutrient resources typically are assumed to change following forest disturbance, usually with nutrient availability increasing initially and subsequently decreasing through later stages of succession. We examined the effects of disturbance (clearcut harvesting with a brief recovery period) on soil organic matter, pH and extractable soil nutrients in successional aspen forests of northern lower Michigan to determine relationships of these variables to changes in herbaceous layer vegetation. Two site types were identified: dry-mesic (glacial outwash sands, low in organic matter) and mesic (calcareous clay till, high in organic matter). Extractable nutrient concentrations were 1.5 to 3 times higher in the A₁ horizon of mesic sites than those of dry-mesic sites. Soil pH and cations increased after disturbance on mesic sites, but not on dry-mesic sites. Patterns of change with disturbance were less pronounced in lower horizons on both site types. Herb-layer species diversity increased after disturbance on mesic sites, but with decreases in the importance of shade-tolerant tree species and *Maianthemum canadense*. Species characteristic of open habitats (e.g. *Pteridium aquilinum*, *Rubus* spp., *Fragaria virginiana*, and *Diervilla lonicera*), increased in importance. Soil factors, species composition and diversity on dry-mesic sites changed little after disturbance, with *Pteridium aquilinum* and ericaceous species remaining dominant in both mature (55-82 yr) and disturbed (≤ 15 yr) stands.

These results suggest that soil nutrient resources do not always change through secondary succession and that patterns of change can be distinctly site-dependent. Disturbance response patterns in the herbaceous layer of these aspen forests are also site-dependent.

Keywords: Clearcutting; Canonical Correspondence Analysis; Disturbance; Plant-soil relationship; Species composition; Species diversity; Secondary succession.

Abbreviations: CCA = Canonical Correspondence Analysis; IVH = Importance Value for Herbs; IVT = Importance Value for Trees; PS = Percentage Similarity; UMBS = University of Michigan Biological Station.

Nomenclature: Gleason & Cronquist (1991).

Introduction

In the past two decades, studies of the ecological significance of disturbance have been directed toward defining a unifying theory of disturbance (White & Pickett 1985). These studies have often emphasized the nature of disturbance (e.g. frequency, size, intensity, severity) and interactions with species' life-history characteristics (Sousa 1984; Canham & Marks 1985). Although the importance of physical environmental factors in determining the response of communities to disturbance has been recognized (White 1979; White & Pickett 1985), these factors often receive little attention in disturbance studies. Given the site-dependence of ecosystem processes and properties, including nutrient cycling and species diversity (Auclair & Goff 1971; Vitousek 1985; Roberts & Gilliam 1995), it is important to assess disturbance and succession processes in relation to site conditions.

Several current models of how plant communities respond to disturbance and develop through secondary succession are based on the assumption that resource availability changes as a result of disturbance and continues to change with time (e.g. Drury & Nisbet 1973; Grime 1977; Tilman 1985; Vitousek 1985). Therefore, an understanding of how soil nutrient availability changes following disturbance and through successional time is needed to predict species change. Nutrient availability frequently increases for a short period immediately following disturbance because of increased decomposition and decreased biological demand, and subsequently decreases through time (Vitousek & Reiners 1975; Bormann & Likens 1979). This has been demonstrated in several studies of nitrogen (see Vitousek et al. 1989), but data are more limited for the other plant nutrients, such as phosphorus and the nutrient cations.

The resource-mediated models of succession provide an explanation for why the responses of plant communities to disturbance are dramatically different on contrasting sites. The response of a species to disturbance is determined ultimately by its ability to obtain

essential resources which may be limiting to varying degrees on different sites (Roberts & Gilliam 1995). Changes in resource availability following disturbance may be strongly influenced by two groups of factors:

1. The nature of the disturbance, in terms of size, intensity and severity, may have pronounced effects on light, temperature, soil moisture and nutrients (Runkle 1985; Collins et al. 1985).

2. Successional changes in stand structure, composition and biotic interactions on forested sites may influence light availability and modify soil fertility or nutrient availability. Change in light availability is directly related to canopy closure, which is a function of stand age and site quality. Modification of soil fertility also may be site-specific, depending on differences in litter chemistry and decomposition.

The response of the herbaceous layer in forests to disturbance in the Great Lakes region has received little attention, particularly with respect to changes in soil characteristics. Ahlgren (1960), Ohmann & Grigal (1979) and Outcalt & White (1981) described the effects of harvesting and/or burning on herb-layer vegetation in the first five years following disturbance. Curtis (1959) discussed weed species composition on highly disturbed sites in Wisconsin, but did not provide information on compositional changes with succession. In northern lower Michigan, Scheiner & Teeri (1981) described changes in species composition and diversity over 53 yr in five stands on one site type (dry-mesic). Albert & Barnes (1987) compared 50-yr-old clearcut plots to uncut plots in northern hardwood stands of western upper Michigan.

Roberts & Christensen (1988) examined compositional variability in relation to soil conditions and successional age in *Populus*-dominated stands in northern lower Michigan. Their study included a broad range of site conditions, disturbance types and stand ages. They found that the tree-shrub layer and the herbaceous layer responded to the same soil factors and that successional sequences differed with site conditions. This study was designed to identify broad compositional patterns, but did not examine in detail the effects of disturbance on species composition and diversity, and soil nutrients. A subset of these same stands was used in the current study to examine detailed patterns of herb-layer and soil response to disturbance. In the current study, we included only recently clearcut or mature stands on one of two distinct site types (dry-mesic and mesic).

The objective of this study was to assess differences in composition and diversity of the herbaceous layer and soil nutrient availability in mature stands and those recently clearcut with a brief recovery period. We compared herb-layer species composition and soil nutrients

in successional *Populus*-dominated forests of northern lower Michigan differing in stand age for two site types: mesic (derived from calcareous clay till) and dry-mesic (derived from glacial outwash sands) (Roberts & Christensen 1988).

Study area

Climate and soils

The study was conducted within a five-county (Cheboygan, Emmet, Charlevoix, Otsego, Montmorency) region of northern lower Michigan. Climatic conditions are relatively uniform throughout the area, with an average annual precipitation of 770 mm and an average annual temperature of 6.2–6.7 °C. Precipitation is distributed relatively evenly throughout the year (Albert et al. 1986).

Soils of the study area are Spodosols derived from parent materials of contrasting glacial origin. Soils on the dry-mesic sites were of the Rubicon series (sandy, mixed, frigid Entic Haplorthods), derived from glacial outwash deposits; mesic soils were of the Montcalm series (sandy, mixed, frigid Alfic Haplorthods), derived from glacial till (Roberts & Richardson 1985; Roberts & Christensen 1988). In general, these soils are acidic and poor in organic matter, with extractable nutrients supplied largely from organic constituents.

Vegetation

The pre-settlement forests within the region were predominantly northern hardwoods with species such as *Fagus grandifolia* and *Acer saccharum* on mesic sites, and coniferous species including *Pinus resinosa*, *P. strobus* and *Tsuga canadensis* on the dry-mesic sites (Kilburn 1957). From 1850 to 1920, extensive logging of the pine and hardwood forests occurred, followed by wildfires (Gates 1930; Kilburn 1957). Thus, the mature stands (55–82 yr old) in the present study are second-growth stands that originated from cutting and burning. The disturbed stands (≤ 15 yr old) originated from clearcutting (without burning) of these mature, second-growth stands.

In our sample, *Populus grandidentata* had the highest importance value for trees (IVT = relative density + relative basal area) on dry-mesic sites, in contrast to mesic sites where *Acer saccharum* shared dominance with *Populus*. Secondary species on dry-mesic sites included *Acer rubrum*, *Quercus rubra*, *Pinus strobus* and *P. resinosa*. On mesic sites, the most important secondary species were *Populus tremuloides*, *Fagus grandifolia*, *Acer rubrum* and *Ostrya virginiana*

(Roberts 1983; Roberts & Christensen 1988).

The vegetation of the herbaceous layer also varied with site type (Roberts 1983; Roberts & Christensen 1988). Dominant species in mature stands on dry-mesic sites were *Pteridium aquilinum*, *Acer rubrum*, and *Vaccinium angustifolium*. On the mesic sites, *Acer saccharum* seedlings, *Pteridium aquilinum*, and *Maianthemum canadense* (a forest herb) were dominant.

Methods

Field methods

Data for this study were taken from 0.1-ha plots (20 m × 50 m), one plot located in each of 52 stands. To examine the effects of disturbance, we compared stands of age 55–82 yr (mature) with stands ≤ 15 yr (disturbed) on both mesic and dry-mesic sites. Stands of *Populus grandidentata* and *P. tremuloides* are considered to reach maturity at 40–50 yr (the pathological rotation age) in this region and stand volume begins to decline beyond this age (Laidly 1990; Perala 1990). This resulted in four disturbance/site classes:

	N	Age range	Median age
Disturbed/mesic	12	3–14 yr	8 yr
Mature/mesic	15	57–82 yr	66 yr
Disturbed/dry-mesic	7	3–12 yr	8 yr
Mature/dry-mesic	18	55–80 yr	70 yr

Stands of at least 0.5 ha area that had not been disturbed since the last stand-initiating disturbance were selected. A single plot was located near the center of each stand in an area that was representative of the stand composition and soil conditions. In each plot, overstory species were sampled as described in Roberts & Christensen (1988). Percent cover of species in the herbaceous layer (all vascular plants < 1 m in height) was visually estimated to within 1% in 25 0.5 m × 2.0 m contiguous quadrats extending along the plot center line. Percent cover and frequency (proportion of quadrats in a plot in which a given species was found) were combined to generate importance values for herb-layer species (IVH = relative cover + relative frequency). Species that occurred within the 0.1-ha plot but not sampled in the 0.5 m × 2.0 m quadrats were assigned an IVH of 0.001.

Four replicate soil samples were taken from three horizons: A₁, A₂, and B₂₁. One sample was taken from a soil pit adjacent to each plot and the other three were sampled with a soil auger at random points along the plot center line. Soil variables (see below) were calculated as mean values for each horizon per plot. We report the results for the A₁ horizon only because the roots of small plants in the herb-layer are concentrated

in this horizon and the patterns for most soil factors were similar in the three horizons.

Laboratory methods

Soil sample preparation followed that of Roberts & Christensen (1988). Although chemical analyses were performed on disturbed (air-dried and sieved) samples, artifactual changes in soil constituents caused by sample preparation are probably slight considering the sandy texture and low organic content of the soil (Gilliam & Richter 1988). Following drying and sieving (2-mm screen), soil samples were analyzed for bulk density, water availability (Percentage moisture content, by weight, between – 0.033 and – 1.5 MPa moisture potential), pH (1:1 soil: H₂O, glass electrode), and organic C (Walkley-Black wet combustion; Black 1965). Samples were extracted with a dilute acid solution (0.05M HCl with 0.0125M H₂SO₄) following Mehlich (1953), a technique well-suited for estimating nutrient availability on acid soils (Gilliam & Richter 1985). Extractable PO₄ was determined by molybdenum blue colorimetry (Mehlich 1953); extractable Ca, K, and Mg were determined by atomic absorption spectrophotometry (Isaac & Kerber 1971).

Data analysis

Canonical Correspondence Analysis (CCA; ter Braak 1987a) was used to determine relationships between species composition and disturbance/site classes. CCA is a constrained ordination technique, in which the ordination axis must be a linear combination of the environmental variables (ter Braak 1987a). For ordination purposes, plots were coded on two environmental dimensions, representing disturbance class (disturbed or mature) and site type (mesic or dry-mesic). For presentation, plots were labelled by disturbance class and site type (disturbed/mesic, disturbed/dry-mesic, mature/mesic, or mature/dry-mesic). The untransformed importance values (IVH) of individual species in the 52 sites were used as the species data. Only species which occurred in ≥ 5 plots were included to reduce the influence of rare species (Gauch 1982; ter Braak 1987b).

Site and species scores on the canonical axes were scaled to mean 0 and sd 1 for symmetrical scaling. Class centroids were located using disturbance/site class means on the individual axes. Disturbance/site class centroids were associated with species by a Euclidian distance metric. CCA attempts to simultaneously locate species maximums and site locations along environmental gradients defined by the measured environmental data. Therefore, it is natural to associate species and sites located similarly along these gradients (ter Braak 1987b).

Table 1. Mean values (\pm SE) of soil variables in the A1 horizon, Shannon-Wiener Diversity Index (H'), and species richness (no. species/plot) for mesic and dry-mesic disturbed and mature stands. Sample sizes are: disturbed/mesic = 12; mature/mesic = 15; disturbed/dry-mesic = 7; mature/dry-mesic = 18.

Disturbance class	C (%)	pH	Ca	K $\mu\text{g}/\text{cm}^3$	Mg	PO ₄	H'	Species richness
<i>Mesic stands</i>								
Young	3.6 (0.5)	5.53 (0.16)	1530 (224)	74 (14)	97 (15)	10.1 (2.9)	3.76 (0.13)	35 (2)
Mature	2.8 (0.3)	4.74 (0.12)	904 (93)	47 (4)	66 (6)	6.7 (0.5)	3.34 (0.16)	26 (2)
	N.S.	***	**	*	*	N.S.	*	**
<i>Dry-mesic stands</i>								
Young	2.3 (0.5)	4.50 (0.14)	419 (52)	56 (14)	43 (8)	3.6 (0.8)	3.04 (0.16)	24 (1)
Mature	1.4 (0.1)	4.45 (0.09)	354 (82)	37 (3)	36 (6)	4.0 (0.5)	2.76 (0.10)	23 (1)
	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.

N.S. = not significant; * = $p < 0.10$; ** = $p < 0.05$, *** = $p < 0.01$.

Two different species lists were used to characterize the vegetation in each class. The first included the 10 species closest to each class centroid (characteristic species) and the second comprised the species with the highest IVHs in each class (dominant species).

Percentage similarity indices (Gauch 1982) were used to assess the relative degree of change in composition among the four disturbance/site classes. Percentage similarity among groups was calculated as the mean of pairwise differences. Herb layer species diversity was determined for each plot using the Shannon-Wiener Diversity Index, H' , and species richness was determined as the total number of species per 0.1-ha plot.

The t -test (PROC TTEST; Anon. 1985) was used for the following comparisons: soil variables between site types by soil horizon; soil variables in the A1 horizon between disturbance classes within site types; and species diversity and richness between disturbance classes within site types.

Results

Soils

Means for all soil variables in the A₁ horizon except potassium (K) were significantly higher ($p < 0.05$) in mesic than dry-mesic soils for disturbed and mature stands combined (Roberts unpubl.). Significant differences between site types were also found in the A₂ and B₂₁ horizons for all variables except bulk density, K and phosphate (PO₄) in the A₂, and K and PO₄ in the B₂₁ horizons (Roberts unpubl.). Such differences underline the importance of the direct or indirect influence of parent materials on these soil variables. Although both soils are Spodosols, dry-mesic soils are derived from

glacial outwash deposits, and consequently are coarse-textured, well-drained, acidic, and infertile. In contrast, mesic soils are derived from glacial till materials with higher clay content, which has resulted in greater water availability and fertility. In addition, species differences on the two site types contribute to differences in litter quality and fertility.

Extractable nutrient data were compared between disturbed stands (≤ 15 yr) and mature stands (55–82 yr) for each site type and soil horizon. There was a consistent pattern of lower mean values for cations in mature stands as compared to disturbed stands on mesic soils (Table 1). These differences were significant ($p < 0.05$) for most cations in the A₁ horizon, but there were virtually no significant differences between disturbance classes for either site type in the A₂ and B₂₁ horizons; thus, these horizons are not presented in Table 1. In contrast, the relatively low concentrations of soil cations in dry-mesic soils did not vary significantly between disturbance classes, regardless of horizon. Extractable P was not significantly different between disturbed and mature stands in any soil horizon on either site type.

Herbaceous layer

With CCA, four significant vegetation axes were extracted accounting for 32 % of the vegetation variance. The first two axes accounted for 17 % of the vegetation variance. Axis 1 was correlated with Site type, $r = 0.866$; axis 2 with Disturbance class, $r = 0.775$. Thus, the constrained CCA analysis allowed a clear partitioning of plots into disturbance/site classes (Fig. 1; Table 2). The remaining variance on axes 3 and 4 may be related to other gradients underlying the vegetation data, such as subtle differences in site conditions. Roberts & Christensen (1988) examined vegetation variation in

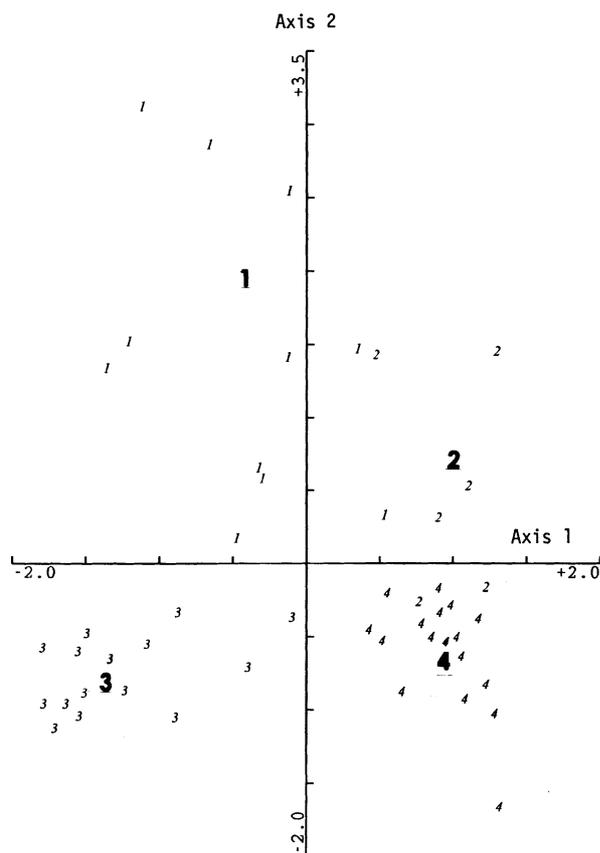


Fig. 1. Canonical Correspondence Analysis ordination of sample plots with disturbance/site classes shown (1 = disturbed/mesic; 2 = disturbed/dry-mesic; 3 = mature/mesic; 4 = mature/dry-mesic). Large numbers indicate positions of the disturbance/site class centroids.

relation to individual soil factors.

The disturbed/mesic plots were characterized by weedy species (e.g. *Taraxacum officinale*, *Poa compressa* and *Rubus* spp.) and species which are typical of moist woods, including *Galium triflorum*, *Osmorhiza claytonii*, *Diervilla lonicera* and *Carex arctata* (Table 3; Gleason & Cronquist 1991). The latter species may have persisted through the disturbance. Several shade-

Table 2. Correlation coefficients between environmental variables (site type and disturbance class) with vegetation axes from CCA.

Environmental variable	Axis	
	1	2
Mesic	-0.866	0.206
Dry-Mesic	0.866	-0.206
Disturbed	0.109	0.775
Mature	-0.109	-0.775

Table 3. Species associated with centroids of disturbance/site groups. The top 10 taxa for each group are listed in order of increasing Euclidean distance from the group centroid.

Disturbance/Site Group Species	Disturbance/Site Group Species
Disturbed/Mesic	Mature/Mesic
<i>Prunus virginiana</i>	<i>Maianthemum canadense</i>
<i>Taraxacum officinale</i>	<i>Abies balsamea</i>
<i>Galium triflorum</i>	<i>Acer saccharum</i>
<i>Rubus</i> spp.	<i>Tilia americana</i>
<i>Osmorhiza claytonii</i>	<i>Lycopodium obscurum</i>
<i>Diervilla lonicera</i>	<i>Acer pensylvanicum</i>
<i>Carex arctata</i>	<i>Polygonatum pubescens</i>
<i>Solidago</i> spp.	<i>Ostrya virginiana</i>
<i>Poa compressa</i>	<i>Smilacina racemosa</i>
<i>Apocynum androsaemifolium</i>	<i>Trillium</i> spp.
Disturbed/Dry-Mesic	Mature/Dry-Mesic
<i>Gaultheria procumbens</i>	<i>Quercus rubra</i>
<i>Hieracium piloselloides</i>	Mosses
<i>Oryzopsis asperifolia</i>	<i>Gaylussacia baccata</i>
<i>Danthonia spicata</i>	<i>Epigaea repens</i>
<i>Oryzopsis pungens</i>	<i>Pinus resinosa</i>
<i>Hieracium venosum</i>	<i>Melampyrum lineare</i>
<i>Monotropa hypopithys</i>	<i>Acer rubrum</i>
<i>Panicum</i> spp.	Unidentified Grasses
<i>Lycopodium tristachyum</i>	<i>Pteridium aquilinum</i>
<i>Pteridium aquilinum</i>	Lichens

tolerant tree species (e.g. *Abies balsamea* and *Acer saccharum*) were associated with the mature/mesic plots, along with shade-tolerant perennial herbs such as *Maianthemum canadense* and *Lycopodium obscurum* (Table 3).

Species associated with the disturbed/dry-mesic plots included the weedy species *Hieracium florentinum* and the cosmopolitan species *Pteridium aquilinum* (Table 3). The remaining characteristic species are all commonly found in dry, open woods (Gleason & Cronquist 1991), including *Gaultheria procumbens*, several grass species and perennial herbs (Table 3). The mature/dry-mesic plots contained several tree species, including *Quercus rubra*, *Pinus resinosa* and *Acer rubrum*. *Pteridium aquilinum* was again associated with this group. Mosses, lichens (mostly *Cladonia* spp.), grasses, and the low shrubs *Gaylussacia baccata* and *Epigaea repens* were also characteristic of the mature/dry-mesic plots (Table 3).

On mesic sites, *Acer saccharum* and *Maianthemum canadense* were the dominant species in the mature stands and decreased in cover and IVH following disturbance (Table 4). Several other shade-tolerant or mid-tolerant tree species, including *Fraxinus americana*, *Acer rubrum*, *Ostrya virginiana*, *Fagus grandifolia* and *Acer pensylvanicum*, showed relatively large decreases

Table 4. Mean percentage cover and importance value (IVH, 0 - 200) of the 19 most important species in the herbaceous layer on dry-mesic and mesic sites by disturbance class.

Site Species	Disturbed			Mature		
	Cover	IVH Mean	(Min - Max)	Cover	IVH Mean	(Min - Max)
Dry-Mesic						
<i>Pteridium aquilinum</i>	51.0	81	(44 - 111)	43.8	84	(41 - 136)
<i>Vaccinium angustifolium</i>	5.3	12	(0 - 41)	3.5	12	(0 - 41)
<i>Gaultheria procumbens</i>	5.2	13	(0 - 45)	0.8	8	(0 - 20)
<i>Acer rubrum</i>	3.2	12	(0 - 39)	4.2	23	(4 - 47)
<i>Danthonia spicata</i>	1.7	6	(0 - 38)	0.1	1	(0 - 7)
<i>Amelanchier</i> spp.	0.8	7	(0 - 12)	0.7	6	(1 - 10)
<i>Carex</i> spp.	1.4	4	(0 - 39)	0.0	0	(0 - 1)
<i>Populus grandidentata</i>	1.0	3	(0 - 40)	0.1	1	(0 - 3)
<i>Quercus rubra</i>	0.7	4	(0 - 12)	1.7	8	(1 - 17)
<i>Rubus allegheniensis</i>	1.0	4	(0 - 27)	0.0	0	(0 - 1)
<i>Oryzopsis asperifolia</i>	1.4	5	(0 - 25)	0.3	2	(0 - 17)
<i>Aster macrophyllus</i>	1.4	3	(0 - 32)	0.0	0	(0 - 1)
<i>Hieracium piloselloides</i>	0.2	2	(0 - 17)	0.1	1	(0 - 7)
<i>Aralia nudicaulis</i>	0.0	0	(0 - 3)	1.9	4	(0 - 54)
<i>Pinus strobus</i>	0.0	0	(0 - 1)	0.8	3	(0 - 18)
<i>Melampyrum lineare</i>	0.0	1	(0 - 5)	0.1	3	(0 - 10)
<i>Pedicularis canadensis</i>	0.0	0	(0 - 0)	1.1	3	(0 - 38)
<i>Diervilla lonicera</i>	1.1	2	(0 - 21)	0.2	1	(0 - 11)
<i>Maianthemum canadense</i>	0.0	0	(0 - 2)	0.3	2	(0 - 24)
Mesic						
<i>Pteridium aquilinum</i>	25.4	43	(0 - 107)	4.3	9	(0 - 54)
<i>Acer saccharum</i>	2.8	13	(0 - 71)	8.5	45	(0 - 93)
<i>Rubus idaeus</i>	2.8	10	(0 - 37)	-	-	-
<i>Fragaria virginiana</i>	4.3	9	(0 - 37)	-	-	-
<i>Rubus allegheniensis</i>	1.6	8	(0 - 23)	0.0	0	(0 - 1)
<i>Rubus</i> spp.	3.3	7	(0 - 55)	0.1	1	(0 - 7)
<i>Fraxinus americana</i>	1.2	7	(0 - 39)	1.9	12	(0 - 62)
<i>Aralia nudicaulis</i>	4.0	6	(0 - 37)	1.7	6	(0 - 34)
<i>Acer rubrum</i>	0.8	6	(0 - 19)	2.2	14	(0 - 41)
<i>Ostrya virginiana</i>	0.6	5	(0 - 18)	3.1	15	(0 - 52)
<i>Diervilla lonicera</i>	1.3	4	(0 - 20)	0.1	0	(0 - 5)
<i>Maianthemum canadense</i>	0.7	3	(0 - 13)	4.0	20	(0 - 64)
<i>Mitchella repens</i>	0.5	2	(0 - 12)	1.1	3	(0 - 27)
<i>Acer pensylvanicum</i>	0.5	1	(0 - 11)	1.3	9	(0 - 44)
<i>Fagus grandifolia</i>	0.1	1	(0 - 5)	2.3	15	(0 - 66)
<i>Amelanchier</i> spp.	0.3	3	(0 - 8)	0.4	4	(0 - 13)
<i>Oryzopsis asperifolia</i>	0.1	1	(0 - 5)	0.3	2	(0 - 9)
<i>Populus grandidentata</i>	0.0	0	(0 - 2)	0.2	3	(0 - 36)
<i>Quercus rubra</i>	0.0	1	(0 - 3)	0.4	2	(0 - 13)

in cover and IVH. *Pteridium aquilinum*, *Rubus* spp. and *Fragaria virginiana* increased dramatically after harvesting.

In contrast to the mesic sites, changes in the dry-mesic stands were less dramatic (Table 4). *Pteridium aquilinum* ranked first in IVH in both disturbance classes and increased only slightly in cover with disturbance. *Vaccinium angustifolium*, *Gaultheria procumbens* and

Acer rubrum ranked second through fifth in both disturbance classes, although both *Vaccinium angustifolium* and *Gaultheria procumbens* had higher cover in the disturbed stands. *Danthonia spicata*, *Carex* spp. and *Rubus allegheniensis* increased in cover and IVH after disturbance.

Species richness and diversity were higher in mesic stands than in dry-mesic stands, and were significantly

($p < 0.05$ - 0.10) lower in mature stands as compared to disturbed stands on mesic sites (Table 1). Richness and diversity showed no relationship to disturbance class in dry-mesic stands (Table 1).

Of the four disturbance/site classes, the disturbed/dry-mesic and mature/dry-mesic classes were most similar in terms of herb-layer composition (PS = 51.3, sd = 14.1). Percentage similarity of the disturbed/mesic and mature/mesic classes was only 19.4% (sd = 12.2). These results support our findings that the change in species composition with disturbance was greater on the mesic sites than the dry-mesic sites.

Discussion

Disturbance-soil nutrient relationships

In the present study, soil pH and exchangeable cations were higher after harvesting on mesic sites, but not on dry-mesic sites where they remained low. Ruark & Bockheim (1988) found similar patterns in an age sequence of aspen stands on sandy outwash (dry-mesic) soils in Wisconsin. In their study, soil nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and organic matter showed no trend with stand age. Magnesium (Mg) was the only nutrient that showed a different pattern; it declined with age (Ruark & Bockheim 1988).

Other studies have highlighted the importance of the forest floor and soil organic matter in nutrient cycling and other ecosystem processes (Covington 1981; Gosz et al. 1976). The role of soil organic matter as a nutrient reservoir is especially important in sandy soils which are inherently low in fertility. In the present study, however, there was no significant difference in organic carbon (C) between the two disturbance classes on either site type.

Following an initial decline after disturbance, surface organic matter should increase with stand age on all sites as biomass accumulates and litterfall increases (Olson 1963; Bormann & Likens 1979; Snyder & Harter 1987). Boose (1986) and Cooper (1981) found this pattern on similar dry-mesic sites from the same study area as ours. Soil organic C content, however, is a function of the rates of decomposition and incorporation of surface organic matter into the soil. On mesic sites, the decomposition rate should decline as regrowth after harvesting occurs. Thus, soil organic C in the A₁ horizon may decline as surface organic matter accumulates (Snyder & Harter 1985). There was a tendency for organic C to increase in the A₂ horizon with stand age ($p = 0.05$; Gilliam & Roberts 1995, unpubl.) on the mesic sites, indicating that downward translocation of organic C may occur over time. A similar pattern was found by

McFee & Stone (1965).

On dry-mesic sites, decomposer organisms are probably limited initially by low soil moisture, low nutrients and high acidity. In addition, the litter on dry-mesic sites contains higher proportions of pine needles and leaves of ericaceous species which are acidic and resistant to decomposition. There is apparently no rapid post-harvest increase in soil organic C and, therefore, no subsequent decrease. Our results do not support those of Boose (1986), who found a decrease in soil organic C with stand age in dry-mesic stands at UMBS. However, he sampled only one stand in each age class and his youngest stand was unusually high in soil organic C.

Disturbance-species diversity relationships

The higher species diversity in recently disturbed stands on the mesic sites is consistent with the findings of Bormann & Likens (1979). They found that species richness was highest in recently clearcut areas, decreased rapidly to a minimum at about 25 - 75 yr, and then began to increase. Our results were not consistent with Peet & Christensen (1988), who found that species richness remained essentially unchanged on fertile sites and increased steadily on infertile sites during the first 80 years of succession. Albert & Barnes (1987) also found higher ground-layer species richness in one 4-yr-old clearcut plot than in 50-yr-old clearcuts in northern hardwood stands.

The differences in species composition between the two disturbance classes on the mesic sites could have been caused by an increase in resource availability, particularly light, in disturbed stands. The most important species in disturbed stands on the mesic sites (Table 4) include *Pteridium aquilinum*, *Fragaria virginiana*, *Rubus idaeus* and *Diervilla lonicera*. These species are characteristic of open habitats, such as dry woods, clearings, meadows, burns, and rocky places (Gleason & Cronquist 1991; Fernald 1970; Marks 1983). The importance values of these species were much lower in the mature stands (Table 4). Seedlings of shade-tolerant tree species such as *Acer saccharum*, *A. rubrum*, and *Ostrya virginiana* were dominant in the mature stands, along with the herbs *Maianthemum canadense*, *Aralia nudicaulis*, and *Mitchella repens* (Table 4). These herbaceous species are characteristic of wooded habitats (Gleason & Cronquist 1991; Fernald 1970).

On dry-mesic sites, species diversity was not related to disturbance class. Species characteristic of open environments, (i.e. *Pteridium aquilinum*, *Gaultheria procumbens*, *Vaccinium angustifolium*, *Amelanchier* spp. and *Acer rubrum*; see Gleason & Cronquist 1991; Fernald 1970) were dominant in both the disturbed and mature stands (Table 4). Given the sensitivity of herb-layer

species composition and biomass to nutrient availability (Gilliam 1988; Gilliam & Turrill 1993), and the fact that nutrient levels are low in mature stands and change little with disturbance on dry-mesic sites, it is not surprising that there is little corresponding change in the species composition of the herbaceous layer. Light levels may also be affected less by disturbance on the dry-mesic sites as indicated by lower tree basal area and canopy density in mature stands on dry-mesic sites relative to mesic sites (Roberts 1983).

In a chronosequence of five stands that were cut and burned on dry-mesic sites at UMBS, species diversity (Simpson index) increased gradually for 25 yr and then remained level to 53 yr (Scheiner & Teeri 1981), followed by a decrease at 70 yr (Scheiner 1988). In the current study, the Simpson index (not shown) was not significantly different between disturbed and mature stands on either site type. The discrepancy between our study and theirs may be related to the fact that our sample included a larger number of stands and that our disturbed stands were harvested but not burned. In addition, the ages of our two disturbance classes may have fallen on either side of the diversity peak, or herbivory by deer, insects or other animals may have removed some species (Curtis 1959; Roberts & Richardson 1985). We saw many of the same changes in individual species on dry-mesic sites observed by Scheiner & Teeri (1981) and Scheiner (1988), however. In all studies, *Carex* spp., *Populus grandidentata*, and *Danthonia spicata* were more abundant in disturbed stands than mature stands, whereas *Acer rubrum*, *Quercus rubra*, and *Pinus strobus* were more common in mature stands. *Pteridium aquilinum* and *Vaccinium angustifolium* maintained dominance in all ages in our study and theirs.

In general, the mature stands on mesic sites were similar in composition to the northern mesic forest described by Curtis (1959) in Wisconsin, although his sites may have been more mesic and nutrient-rich. One notable difference was the greater abundance of *Pteridium aquilinum* in our mature mesic stands. Because Curtis (1959) sampled only undisturbed stands, many of his stands were probably older than ours. We would expect *Pteridium aquilinum* to gradually decline in our mature stands with time. Several of the most important herbaceous species in our mature dry-mesic stands, including *Pteridium aquilinum*, *Vaccinium angustifolium*, and *Aralia nudicaulis* were also listed by Curtis (1959) as prevalent species in the northern dry forest and northern dry-mesic forest of Wisconsin. Our dry-mesic sites may have been more nearly equivalent to his dry forest sites and our mesic sites closer to his dry-mesic sites.

Acknowledgements. We thank Dr. D.M. Gates and M. Paddock for the use of facilities of the University of Michigan Biological Station and for their support. The assistance of the Michigan Department of Natural Resources in locating sample stands is appreciated. We are indebted to A. Levenson, A. Hainault, and T. Paddock for assistance in the field and to F. Forrester and W. Snavley for typing the manuscript. The invaluable assistance of Lawrence Wuest with multivariate analysis is greatly appreciated. We thank Scott Gleeson, George Parker, and anonymous reviewers for helpful suggestions on the manuscript. We are grateful to Robert Peet for editorial comments that improved the quality of the manuscript. This work was supported in part by grants from Duke University, Sigma Xi, and the Atlantic Richfield Co. Foundation.

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Received 29 June 1994;

Revision received 25 September 1995;

Accepted 1 October 1995.