Establishment of unique herbaceous plant communities on tree tip-up mounds in Michigan's Upper Peninsula

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Abstract

Windthrow disturbances create tree tip-up mounds that increase structural heterogeneity and resource availability in forests. Novel plant communities may form quickly on tip-up mounds, but evidence is varied and limited. In this study, I tested the hypothesis that tip-up mounds have higher herbaceous species richness and unique herbaceous plant assemblages compared to reference plots on the forest floor. I assessed species richness and percent cover by species on 25 tip-up mounds in a northern mesic forest. Cover of one herbaceous species, *Convolvulus arvensis*, was significantly higher on the top and upper mound surfaces compared to closed canopy reference sites, but species richness did not differ between any sites. Distinct herbaceous communities seemed to form on mounds and reference plots, but statistical verification was beyond my abilities. My results add to the limited literature on herbaceous tip-up mound communities and highlight the importance of tree tip-up mounds when considering forest diversity.

Introduction

Localized disturbance is an important aspect of forest health worldwide. Disturbances promote diverse biological communities by increasing habitat heterogeneity and opening new sites for colonization (Thompson 1980). Wind is a key agent of local disturbance in forests. Windstorms can knock down entire trees, creating canopy gaps and tip-up mounds. Depending on the severity of the storm, they can also cause heavy mortality and reduce tree density size and structure. Consequently, wind disturbance can alter important ecological processes such as succession (Dale et al. 2001). Succession is the process by which different communities periodically occupy a given environment. Resource availability, the physiology of different plant species, and different types of disturbance can all influence successional changes in species composition and structure (Christiansen 2003). In the context of localized wind disturbances, the formation of canopy gaps and tip-up mounds may set succession back to an early successional state characterized by faster rates of soil nutrient consumption and plant species with shorter lifespans (Bazzaz 1979).

Large tip-up mounds form when trees uproot as they fall, heaving masses of soil up with them. Tip-up mounds experience a distinct set of environmental and ecological conditions, making them unique habitats within the greater forest ecosystem (Beatty 2003). The combined effects of increased exposure to weathering, decreased exposure to competition, and browsing complicate our understanding of tip-up mounds as potential havens for novel plant communities. Peterson et al. (1990) found that soil moisture, soil temperature and sunlight vary significantly between tip-up mound and undisturbed soil sites. Specifically, mounds experience drier conditions, more extensive erosion, and quicker freezing and thawing in the winter compared to adjacent areas (Beatty 1984; Peterson et al. 1990). While these conditions may be unfavorable for plant recruitment, soil disturbance can promote seed germination and seedling growth, and increased light availability atop mounds can favor different species than on undisturbed soil surfaces (Sauer and Struik 1964; Peterson and Pickett 1995; Putz 1983). Tip-up mounds can also act as refugia from vertebrate herbivores and convenient landing sites for avian species that promote seed dispersal (Long et al. 1998; Thompson 1980).

Unique vegetation often occurs on older mounds that have stabilized over several decades (Beatty 2003). However, the establishment of novel communities on newly-formed mounds remains poorly understood. Studies on younger, less stable tip-up mounds are sparse and do not agree on whether or not novel assemblages form rapidly on new mounds. Lang et al. (2009) found that species richness and cover of some herbaceous species were higher on mounds, which increase structural complexity and homogenize soil resources. In contrast, Spicer et al. (2018) found no difference in plant communities between tip-up mounds and undisturbed sites, and Peterson et al. (1990) found lower diversity and plant cover on mounds. These three studies were conducted in temperate mixed forests in the eastern United States and only considered mounds less than 25 years old. Further studies of wind disturbance and tip-up mounds are particularly relevant in the eastern United States and similar regions because wind is often considered the most important agent of abiotic disturbance in eastern U.S. forests (Dale et al. 2001; Peterson 2000).

My study sought to describe how herbaceous plant communities vary between tip-up mounds and reference sites in a temperate forest in Michigan. To do so, I identified and estimated the cover of herbaceous plants found on tip-up mounds and corresponding reference sites on undisturbed ground. Tip-up mounds contain at least six microsites, defined as small areas that noticeably differ from their immediate surroundings (Figure 1). I surveyed two microsites on each tip-up mound: the top surface of the mound and the side of the mound connected to the trunk of the fallen tree (referred to as the upper mound surface). I hypothesized that tip-up mounds differ in herbaceous species richness compared to adjacent areas and the surrounding forest matrix, and that mounds have unique plant assemblages compared to reference sites.

Methods

Study environment

I conducted this study at the University of Notre Dame Environmental Research Center (UNDERC) in Gogebic County, Michigan. Forests at UNDERC are largely second-growth northern mesic forest. Specifically, I studied tip-up mounds within two blowdowns that resulted from the same windstorm in July 2016 (M. J. Cramer, *pers. comm.*). Blowdowns refer to clusters of trees that have been blown down by the wind. This storm created tree tip-up mounds between 1 and 3 meters tall.

Vegetation sampling

I measured the length and width of the top surface of 25 tip-up mounds and estimated the area of each mound's top surface. I used this area to determine the plot size for sampling the upper surface of the mound and two randomly selected reference sites on undisturbed soil. I repeated this process for each individual tip-up mound. Sampling involved identifying and counting the number of species present, and visually estimating the percent cover by species within each plot. The first reference site was adjacent to the mound, chosen 2 meters away from the mound and beneath the canopy gap created by the treefall. The second reference site was beneath nearby closed canopy forest, 2 meters away from the edge of the canopy gap (Figure 1).

Analyses

I used a one-way ANOVA test to compare mound microsites and reference plots for species richness. Because of non-normal data, I used Kruskal-Wallis tests to compare total herbaceous plant cover and cover of the two most abundant herbaceous species: *Convolvulus arvensis* and *Galeopsis tetrahit*. I further analyzed significant Kruskal-Wallis results with Nemenyi's test of multiple comparisons. Nemenyi's test is the nonparametric equivalent of the Tukey test, a post-hoc test that determines specific pairwise differences among groups. All analyses were conducted using R version 3.5.1 (R Core Team).

Results

Herbaceous species richness

Species richness ranged from 0 to 5 herbaceous species across the four microsites. The intact reference and upper mound surface had the greatest mean species richness (Figure 2). However, I found no significant differences in herbaceous species richness between the top mound surface, upper mound surface, intact ground reference and closed canopy reference sites ($df = 3$, $F = 1.92$, $p > 0.1$).

Herbaceous cover

Total herbaceous plant cover was greatest on the intact and closed canopy reference sites, but I found no significant differences in total cover across the four microsites ($df = 3$, $H = 2.33$, $p > 0.5$). Cover of *Galeopsis tetrahit* was greatest on the top mound surface and closed canopy reference, but I found no significant differences in *G. tetrahit* cover between microsites ($df = 3$, $H = 14.13$, $p > 0.5$). Cover of *Convolvulus arvensis* was significantly higher on the top and upper mound surfaces than the closed canopy reference ($df = 3$, $H = 14.13$, $p < 0.05$). On average, the top mound surface had 74% more *C. arvensis* cover than the closed canopy reference (mean rank difference = 21.34, $p < 0.05$), and the upper mound surface had 79% more *C. arvensis* cover than the closed canopy reference (mean rank difference = 25.82, $p < 0.01$) (Figure 2).

The herbaceous plant assemblages that occurred on tip-up mounds contrasted with those on reference sites. Mounds were dominated by *Convolvulus arvensis* and *Galeopsis tetrahit*, whereas reference sites hosted *Convolvulus arvensis*, *Galeopsis tetrahit*, and a wider variety of sedges and ferns (Figure 3).

Discussion

In accordance with part of my hypothesis, my results suggest that distinct herbaceous assemblages may form on young (2-3 years old) tree tip-up mounds at the University of Notre Dame Environmental Research Center. *Convolvulus arvensis* cover was significantly higher on tip-up mound microsites, and a qualitative examination showed unique herbaceous communities on mounds compared to reference plots, though statistical tests of whole-community differences were beyond the scope of this study. *C. arvensis* cover may have been higher on mounds because their extensive root systems and sprawling habit allow them to spread above and below ground, and resist severance. Furthermore, *C. arvensis* can spread by both seeds and root or rhizome fragments, enabling them to colonize new areas rapidly (Weaver and Riley 1982). The larger assortment of ferns and sedges found on reference sites could be due to the fact that tip-up mound microsites are drier and elevated above the undisturbed forest floor (Beatty 1984). Ferns require high moisture for sexual reproduction, and although they can reproduce asexually through rhizomes, perhaps these rhizomes are unable to climb up through tip-up mounds.

Similarly, sedges may be restricted by their reliance on vegetative reproduction through rhizomes as their primary method of spreading (Chen et al. 2015).

On the other hand, herbaceous species richness did not differ between tip-up mound microsites and reference plots. This may be because the herbaceous species I observed do not particularly benefit from wind-related disturbances and tip-up mound conditions. Compared to woody species, many herbaceous species experience less browsing pressure. Browsing can induce stress and reduce seed production in browse-intolerant plants (Allison 1990). The herbaceous species I observed also lack fruits that promote the spread of seeds by avian frugivores that may use tip-up mounds as landing sites (Thompson 1980; Long et al. 1998). Similar studies found various results for species richness in tip-up mound microsites and reference plots. Peterson and Leach (2008) found higher species richness on forest floor plots compared to mounds, while Lang et al. (2009) found higher species richness on mounds. Therefore, differences in species richness between tip-up mounds and reference plots remain unclear. My results do, however, add to the small number of studies that advocate for the formation of unique plant communities on recently formed mounds (Palmer et al. 2000; Hutnik 1952), while also providing a focus on herbaceous species.

Future studies could sample all six microsites (Figure 1) associated with tip-up mounds, which builds upon the methodologies of both Hutnik (1952) and Peterson et al. (1990). No studies of tip-up mound habitats have sampled more than four of these microsites. Future studies can also increase our understanding of tip-up mounds by expanding the spatial and temporal scales of tip-up studies. For example, studying tip-up mounds in different types of forests would clarify the extent to which mounds promote forest diversity, as most tip-up studies are concentrated in temperate forests (Betras et al. unpublished). Different forests and plant species also exhibit differential vulnerability to wind events due to factors like stand density and root depth (Dale et al. 2001). Repeated sampling of tip-up mounds would help because tip-up mound communities change and microsite plant community composition can converge over time (Mollaei Darabi et al. 2014; Palmer et al. 2000).

This study has important implications for forest management and restoration. In general, tree-falls promote diversity in forests by creating gaps in the canopy and increasing the heterogeneity of the landscape. Newly-formed tip-up mounds interrupt mono-specific patches of undergrowth and allow different species to establish themselves by creating novel habitats (Thompson 1980). Although small-scale wind events are difficult to model and predict, Dale et al. suggests that windstorm characteristics change alongside our rapidly changing climate. Berz (1993) further speculates that the frequency and intensity of tornadoes and extreme storms will increase with the effects of climate change. By improving our understanding of tip-up mounds and their associated microsites, we can better inform management efforts such as salvage logging, and better understand how natural disturbances and novel habitats contribute to the diversity of forest ecosystems.

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Figures

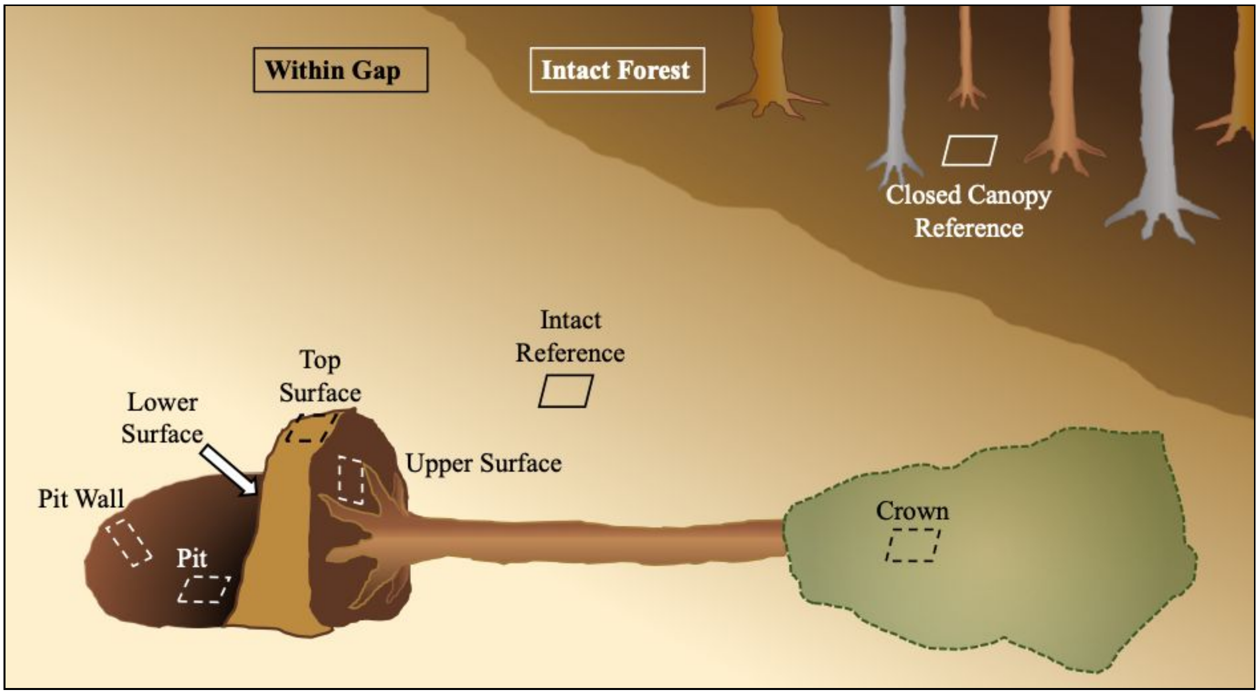

Figure 1. Tip-up mound and surrounding habitat that occur within a stand of continuous forest. Windstorms typically create multiple clustered tree-falls with tip-up mounds. Tip-up mounds contain at least six distinct microsites (dashed rectangles), though I surveyed two: Top Surface and Upper Surface (Betras et al. unpublished). Two contrasting types of reference sites are depicted by solid rectangles.

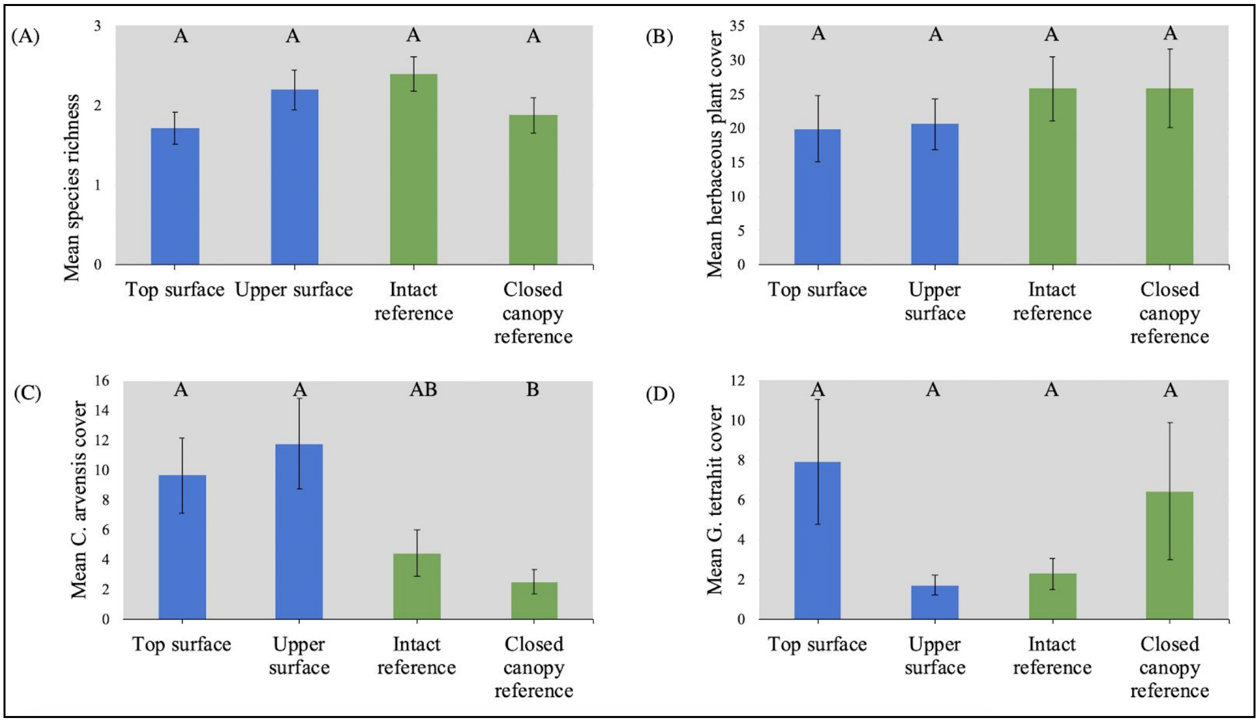

Figure 2. Mean cover of *Convolvulus arvensis* (± SE) was significantly higher on the top mound surface and the upper mound surface versus closed canopy reference plots (C) at the University of Notre Dame Environmental Research Center (Kruskal-Wallis test, $p < 0.05$; Nemenyi post-hoc test, $p < 0.05$). Mean species richness (A), total herbaceous plant cover (B), and cover of *Galeopsis tetrahit* (D) were not significantly different.

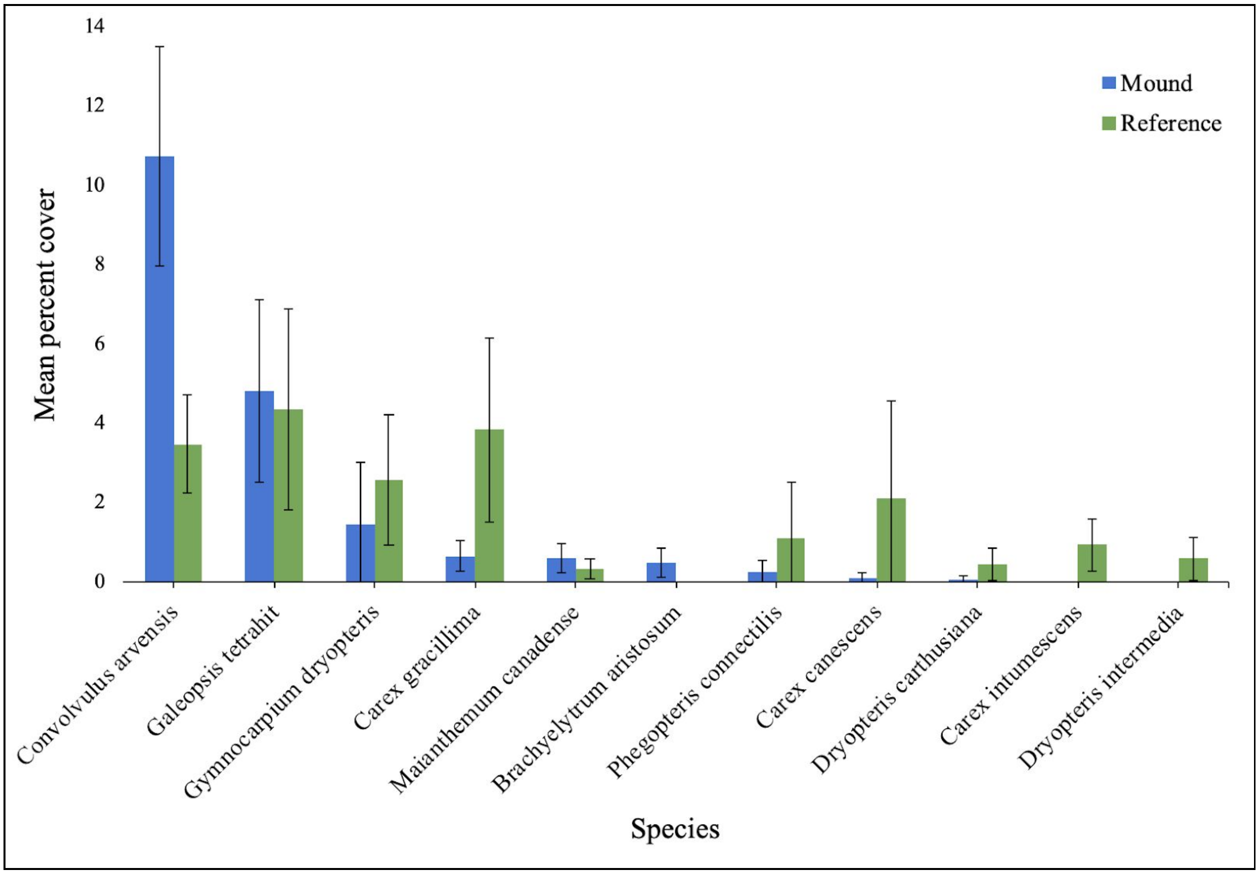

Figure 3. Mean percent cover (± SE) by species and plot type at the University of Notre Dame Environmental Research Center. Only species representing more than 0.5% mean cover on either tip-up mounds or reference plots are included here.

Appendix

Raw data collected and used in this study.

Mound	Scientific name	Top surface	Upper surface	Intact ref	Closed canopy ref
1		%	%	%	%
	Convolvulus arvensis	25	10		7
	Gymnocarpium dryopteris			10	
	Galeopsis tetrahit			3	5
2		%	%	%	%
	Convolvulus arvensis	5	10	1	
	Brachyelytrum aristosum		5		
	Carex deflexa		3		
3		%	%	%	%
	Convolvulus arvensis	8	6	6	
	Gymnocarpium dryopteris	6	55		9
4		%	%	%	%
	Maianthemum canadense	2	2	3	
	Convolvulus arvensis	4	5		
	Carex gracillima	4	6	8	
	Dryopteris carthusiana		3		
	Carex intumescens			1	
	Dryopteris intermedia				15
5		%	%	%	%
	Carex gracillima	5	5		
	Maianthemum canadense	3	5		
	Trientalis borealis			5	3
	Carex gracillima				7
6		%	%	%	%
	Convolvulus arvensis	1	5	1	
7		%	%	%	%

	Convolvulus arvensis	1	3		
	Galeopsis tetrahit		4		
	Carex gracillima			3	
	Dryopteris intermedia			3	
	Gymnocarpium dryopteris				40
8		%	%	%	%
	Convolvulus arvensis	2	5	20	5
	Gymnocarpium dryopteris	1	9	40	
	Galeopsis tetrahit			4	
	Dryopteris carthusiana			6	
	Carex canescens				85
9		%	%	%	%
	Galeopsis tetrahit	1		2	5
	Convolvulus arvensis	1	5	3	15
	Gymnocarpium dryopteris			10	
	Carex laxiflora				5
10		%	%	%	%
	Convolvulus arvensis	15	5		
	Galeopsis tetrahit	5	2	15	7
	Gymnocarpium dryopteris				3
	Carex gracillima			55	3
11		%	%	%	%
	Convolvulus arvensis		5	7	
	Galeopsis tetrahit		2	7	5
	Carex gracillima			20	55
	Gymnocarpium dryopteris				10
12		%	%	%	%
	Galeopsis tetrahit	2	3	10	20
	Carex gracillima	3		3	
	Convolvulus arvensis	3	5	3	2

	Athyrium filix-femina			3	20
13		%	%	%	%
	Convolvulus arvensis	50	40	7	
	Galeopsis tetrahit	32	3		
	Carex gracillima		10		5
	Carex intumescens				8
14		%	%	%	%
	Caulophyllum thalictroides			3	
	Convolvulus arvensis	20	37		4
	Galeopsis tetrahit	50	7	7	4
	Carex gracillima			25	3
	Gymnocarpium dryopteris				7
	Actaea pachypoda				6
15		%	%	%	%
	Convolvulus arvensis	25	40	3	7
	Galeopsis tetrahit	55	10	6	15
	Carex gracillima			5	
16		%	%	%	%
	Convolvulus arvensis	30	50	20	6
	Galeopsis tetrahit	7	2		
	Unidentified herb 1	3			
	Unidentified fern 1		1		
	Galeopsis tetrahit			5	
	Dryopteris intermedia				12
17		%	%	%	%
	Convolvulus arvensis	8	35	30	12
	Galeopsis tetrahit	4		1	15
	Verbascum thapsus			2	
	Carex laxiflora			7	
18		%	%	%	%

	Convolvulus arvensis	15	12	8	5
	Galeopsis tetrahit	7	5	2	85
	Gymnocarpium dryopteris		2		
	Phegopteris connectilis		4		
	Unidentified fern 1			2	
19		%	%	%	%
	Maianthemum canadense			3	1
	Lysimachia borealis		2	6	
	Galeopsis tetrahit		2		
20		%	%	%	%
	Dryopteris carthusiana			5	
	Phegopteris connectilis		9	50	
	Schizachne purpurascens				10
	Maianthemum canadense				8
	Erythronium americanum				1
	Urtica dioica	10	18		
	Convolvulus arvensis	7	3		
	Unidentified Agrostis spp. 1	3			
	Brachyelytrum aristosum		5		
21		%	%	%	%
	Convolvulus arvensis	3	8		
	Galeopsis tetrahit	10			
	Unidentified Gallium spp. 1		6	3	
	Carex intumescens			20	
	Carex deflexa				2
22		%	%	%	%
	Caulophyllum thalictroides				2
	Urtica dioica		7		
	Convolvulus arvensis	18	5		
	Carex canescens	5			

	Maianthemum canadense		3		
	Dryopteris carthusiana			12	
	Unidentified Dryopteris spp. 1			5	
	Unidentified herb 2			15	
	Carex intumescens			5	
	Unidentified Gallium spp. 1				7
23		%	%	%	%
	Carex canescens			20	
	Trillium cernuum				1
24		%	%	%	%
	Maianthemum canadense	10	5		2
	Galeopsis tetrahit	25	3		
	Unidentified fern 1		4		
	Trientalis borealis		1		
	Trillium cernuum		1		
	Brachyelytrum aristosum	5	10		
	Phegopteris connectilis			5	
	Convolvulus arvensis			2	
	Schizachne purpurascens			12	
25		%	%	%	%
	Carex intumescens			8	5
	Athyrium filix-femina				8