

Species composition on tipup mounds and pits created by catastrophic windthrow in a Minnesota forest

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Abstract. We recorded the presence of vascular plant species on microsites generated by the nearly complete windthrow of a *Pinus strobus* forest. We classified microsites as unaltered forest floor, old soil uplifted with the root mass, soil on the mound which was newly exposed, and the pit. Ruderal species (e.g. *Chenopodium album*, *Verbascum thapsus*, *Conyza canadensis*) were most frequent in the new soil microsites, but only once had > 10% frequency in the unaltered forest floor quadrats. Species composition of old soil microsites was intermediate between that of forest floor and new soil microsites. *Dryopteris carthusiana* and animal burrows were more frequent in the pits than in other microsites. Canonical Correspondence Analysis indicated that the species composition of the four microsites differed in the first years after the disturbance. 14 yr later, the communities on the microsites have converged to a similar species composition, which is distinct from the pre-disturbance forest floor community, and similar to the current forest floor community.

Keywords: Convergence; Disturbance. Habitat heterogeneity; Microsite; Topography.

Nomenclature: Kartesz (1994).

Introduction

Catastrophic windthrow of forest trees may create tipup mounds and pits, thus disturbing the ground layer and creating microsite heterogeneity (Foster 1988; Schaetzl et al. 1989b; Peterson et al. 1990). Vascular plant species have differential success on the different types of microsites (Ellison et al. 1993; Henry & Swan 1974; Putz 1983; Webb 1988; Peterson & Pickett 1990), due to differing physical and chemical processes/properties operating therein (Beatty 1984; Schaetzl et al. 1989a; Peterson et al. 1990; Carlton & Bazzaz 1998a; Denslow et al. 1998). Differences in species composition among the microsites may remain over time as succession occurs on the site as a whole, or the microsites

may converge in species composition due to increasing similarity in environmental conditions. There are few long-term studies on tipups beginning immediately after catastrophic windthrow, and processes occurring on recent tipups may be different from those on long-established tipups (Beatty 1984; Peterson & Campbell 1993).

We followed vascular plant species on pits and mounds and intact forest floor quadrats from two weeks until 14 yr after the storm event. We studied whether species responded to the type of microsite created by the uprooted trees and whether the species composition changed through time.

Methods

The study site, the Cedar Creek Natural History Area (CCNHA), is a U.S. National Science Foundation Long Term Ecological Research site in Anoka and Isanti Counties, Minnesota. On July 3, 1983, straight line winds associated with a large thunderstorm blew down portions of several forests in CCNHA. Before the storm, the forest was dominated by *Pinus strobus* and *Betula papyrifera*, with a total density of 1104 stems/ha, and a basal area of 42m²/ha. The forest floor was essentially flat and no old tipups were visible (pers. obs.). It is likely that the trees colonized an old field. The storm reduced the forest to a density of 446 stems/ha, and a basal area of 12 m²/ha. 14 yr later, the site had a few, large *Pinus* remaining, and the young canopy is dominated by *Fraxinus nigra*, *Quercus rubra* and *Prunus serotina* (Arévalo et al. this volume)

We established 120 randomly located quadrats (1 m × 1 m) on the 'forest' floor within two weeks after the storm of July 1983. These were permanently marked in the two diagonal corners with iron reinforcement bars. As we could not guarantee the exact dates of revisits, we chose to record only the presence of vascular plant species. The quadrats were surveyed in July 1983, which is assumed to reflect pre-disturbance vegetation, and resampled in July of 1984, 1985, 1990, 1993 and 1997. The presence of vascular plant species rooted in the new and old soil of the 56 tipups was recorded beginning in 1984; the pit vegetation was sampled beginning in 1985. New soil encompassed all the disturbed soil above the level of the forest floor, and is equivalent to the 'mound + plate + under' of Carlton & Bazzaz (1998b), or the 'mound' of Peterson et al. (1990). Old soil was that portion of the forest floor which had been uplifted, often to near vertical, but retained its soil structure intact, at least at first, thus is equivalent to the 'TOP' of Carlton & Bazzaz (1998b). In the present study, pit included all exposed soil below the level of the forest floor, thus equivalent to the 'pit + wall' of Peterson et al. (1990).

The species data were ordinated with Canonical Correspondence Analysis (CCA; ter Braak 1987) using Canoco 4 for Windows (ter Braak & Šmilauer 1998). Explanatory variables were all dummy (1/0) variables representing the type of microsite (pit, new soil, old soil, forest floor quadrats), separated by year. These dummy variables are represented by their centroids, along with species scores, on ordination biplots.

Results

Canonical Correspondence Analysis indicated that in the early years of this study (top of Fig. 1), the microsites differed in species composition. Old soil plots were similar to the forest floor quadrats, and pits were more similar to old soil than new soil plots. The close positioning of all of the centroids from 1997 in the bottom of Fig. 1 indicates that the species composition of the microsites has converged through time. Species scores illustrate taxa typical of new soil in the upper right of Fig. 2, those most frequent in forest floor quadrats on the upper left, and those that increased in all microsites on the lower left.

Prior to the windthrow, *Amphicarpaea bracteata*, *Carex pensylvanica*, *Maianthemum canadense*, *Parthenocissus quinquefolia*, and *Rubus idaeus* all had > 35% frequency in the forest floor quadrats (Table 1). In the first two years after the storm, these species remained at about the same frequency, except *Maianthemum*, which doubled. CCA species scores for these species are located in the upper middle left portion of Fig. 2. Many of the less frequent species increased their frequency. In this period the new soil quadrats were dominated by ruderal species; vines (*Vitis riparia*, and *Parthenocissus*) and the clonal *Rubus idaeus* were also frequent.

Carex pensylvanica, *Chenopodium album*, *Conyza canadensis*, *Verbascum thapsus* and *Polygonum cilinode* all more than doubled their frequency in old soil plots by 1985. Two years after the storm, *Parthenocissus* and *Rubus* were present in more than half of the plots and *C. canadensis* was present in one third.

In 1990 and 1993 several species – *Urtica dioica*, *Hackelia deflexa* – increased strongly in frequency in all microsites, only to decline again by 1997. *Pinus strobus* seedlings also followed this pattern. CCA species scores of these taxa are in the lower middle of Fig. 2.

By 1997, two additional species – *Dryopteris carthusiana* and *Polygonum cilinode* – had joined the five common forest floor species in all four microsites (Table 1). They also had > 35% frequency.

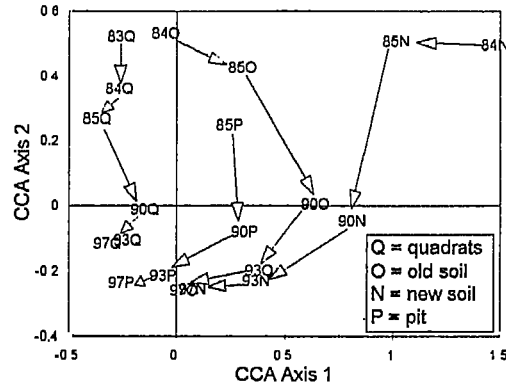


Fig. 1. CCA-diagram: centroids of microsite type, by year. The first two digits of the centroid label represent the year of study, and the letter represents the microsite type. Arrows connect subsequent sampling episodes.

Discussion

In the first two years after the storm the four microsite types had clear differences in species composition. As found by Carlton & Bazzaz (1998a), the initial type and amount of soil disturbance which occurred in the storm strongly influenced recruitment patterns. The bare mineral soil in the new soil plots was initially colonized by ruderal species (these may have been either from activation of the seed bank (Putz 1983) or from wind dispersal into the site (Nakashizuka 1989; Peterson et al. 1990)). Species composition in the old soil plots initially was similar to undisturbed forest floor quadrats. Species composition in pits was (unlike Carlton & Bazzaz 1998a), more similar to that of old soil than new. This is perhaps due to the sandy well-drained soil (preventing localized flooding as was found by Putz 1983; Cornett et al. 1997), to the dense shade hindering establishment of ruderals, and to vegetative ingrowth of forest floor plants.

The plant communities in these four microsites were

Table 1. Frequency (in percent) of species with at least 200 occurrences, by year and microsite type, in order of declining frequency.

Species	Forest Floor Quadrats						New Soil on Mounds					Old Soil on Mounds					Pits			
	1983	1984	1985	1990	1993	1997	1984	1985	1990	1993	1997	1984	1985	1990	1993	1997	1985	1990	1993	1997
<i>Rubus idaeus</i>	92.5	91.7	93.3	89.2	91.7	92.5	46.0	84.3	92.6	90.7	89.1	84.9	96.3	91.1	92.9	94.6	60.0	92.3	85.2	90.6
<i>Parthenocissus quinquefolia</i>	89.2	85.8	91.7	91.7	93.3	91.7	60.0	54.9	48.1	72.2	85.5	67.9	87.0	64.3	76.8	87.5	55.6	51.9	61.1	79.2
<i>Amphicarpaea bracteata</i>	60.8	51.7	64.2	74.2	71.7	70.8	14.0	5.9	9.3	48.1	60.0	32.1	35.2	30.4	41.1	48.2	17.8	30.8	59.3	58.5
<i>Carex pensylvanica</i>	37.5	38.3	39.2	54.2	55.8	43.3	10.0	21.6	44.4	55.6	49.1	13.2	35.2	50.0	66.1	58.9	15.6	40.4	40.7	28.3
<i>Maianthemum canadense</i>	32.5	42.5	59.2	55.8	60.0	66.7	0.0	2.0	16.7	29.6	38.2	20.8	38.9	25.0	33.9	41.1	6.7	23.1	37.0	41.5
<i>Polygonum cilinode</i>	0.8	8.3	8.3	52.5	68.3	68.3	10.0	7.8	44.4	63.0	72.7	1.9	14.8	57.1	66.1	76.8	13.3	40.4	55.6	67.9
<i>Pinus strobus</i>	26.7	13.3	18.3	67.5	62.5	29.2	12.0	9.8	77.8	70.4	40.0	5.7	11.1	50.0	53.6	28.6	2.2	61.5	42.6	22.6
<i>Urtica dioica</i>	15.0	21.7	19.2	22.5	40.0	31.7	8.0	5.9	33.3	48.1	45.5	13.2	20.4	19.6	60.7	46.4	22.2	23.1	37.0	28.3
<i>Conyza canadensis</i>	0.0	9.2	3.3	12.5	5.8	3.3	80.0	64.7	68.5	64.8	36.4	1.9	42.6	66.1	73.2	25.0	33.3	51.9	16.7	3.8
<i>Arisaema triphyllum</i>	3.3	25.0	28.3	41.7	47.5	45.8	0.0	0.0	5.6	18.5	27.3	7.5	9.3	10.7	12.5	25.0	11.1	21.2	35.2	45.3
<i>Dryopteris carthusiana</i>	0.0	12.5	12.5	14.2	25.0	34.2	0.0	0.0	9.3	55.6	65.5	0.0	1.9	10.7	50.0	66.1	15.6	30.8	48.1	54.7
<i>Aquilegia canadensis</i>	20.8	22.5	25.0	26.7	29.2	24.2	2.0	7.8	16.7	24.1	20.0	17.0	18.5	28.6	30.4	23.2	20.0	34.6	29.6	18.9
<i>Vitis riparia</i>	14.2	15.0	15.0	21.7	40.8	20.8	20.0	9.8	27.8	37.0	12.7	15.1	16.7	25.0	42.9	16.1	0.0	32.7	42.6	15.1
<i>Toxicodendron radicans</i>	13.3	22.5	22.5	27.5	30.8	31.7	0.0	0.0	9.3	14.8	18.2	11.3	11.1	14.3	23.2	25.0	6.7	19.2	24.1	26.4
<i>Gallium triflorum</i>	21.7	40.8	33.3	14.2	35.0	29.2	6.0	5.9	1.9	14.8	16.4	3.8	7.4	0.0	17.9	10.7	15.6	5.8	20.4	18.9
<i>Aralia nudicaulis</i>	13.3	25.8	25.8	22.5	23.3	23.3	2.0	3.9	16.7	18.5	23.6	13.2	13.0	17.9	19.6	23.2	6.7	9.6	7.4	24.5
<i>Hackelia deflexa</i>	0.0	18.3	13.3	35.0	40.0	15.8	10.0	7.8	22.2	33.3	9.1	7.5	5.6	19.6	32.1	3.6	8.9	15.4	20.4	15.1
<i>Quercus ellipsoidalis</i>	17.5	20.0	15.8	25.0	29.2	29.2	0.0	0.0	1.9	7.4	12.7	0.0	1.9	1.8	12.5	26.8	2.2	5.8	7.4	24.5
<i>Anemone quinquefolia</i>	1.7	2.5	34.2	37.5	28.3	26.7	0.0	0.0	0.0	9.3	3.6	1.9	1.9	8.9	17.9	12.5	6.7	17.3	9.3	20.8

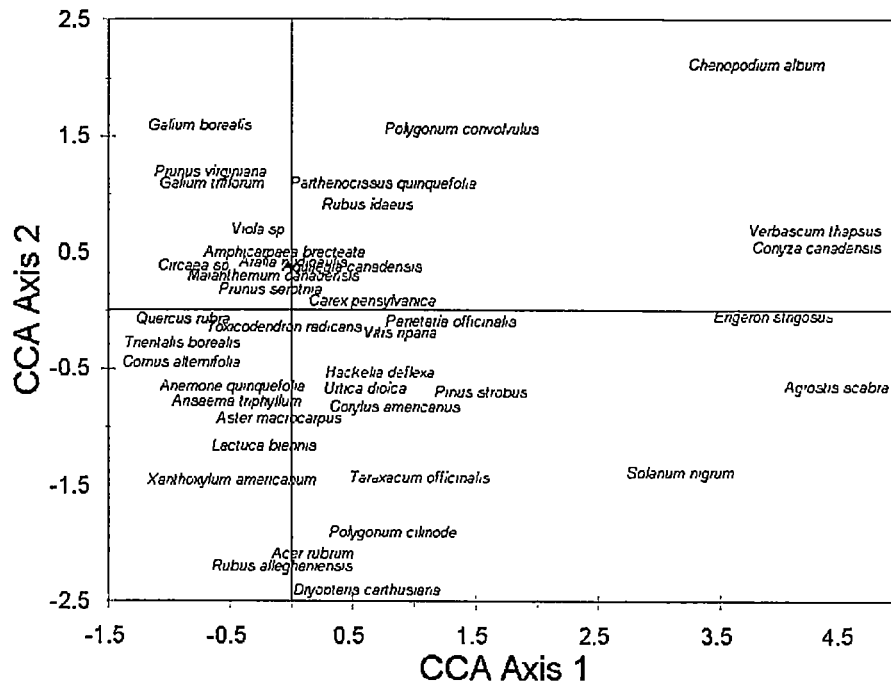


Fig. 2. CCA-diagram: species scores for the 40 most frequent species from the same ordination as in Fig. 1. Note difference in scale of the axes.

quite dynamic over the study period, particularly in the first 7-10 years. Rapid changes on tipups in the first few years were also found by Peterson et al. (1990), Putz (1983) and Núñez-Farfán & Dirzo (1988). Such dynamics are likely due to continue, albeit at a slower pace, as a result of erosion of the mounds, soil sloughing into pits, burrowing of animals, as well as successional changes (Jonsson & Esseen 1990; Peterson et al. 1990; Denslow et al. 1998).

After 1990 the microsite types began to converge, although they were distinct for several more years. By 1997 the initial differences in species composition among the microsites were nearly gone. Such convergence is perhaps explained by processes such as soil formation in the disturbed microsites (Carlton & Bazzaz 1998a; Denslow et al. 1998). This is somewhat contrary to most studies of older tipups in which differences in species composition remain for decades (Beatty 1984; Peterson & Campbell 1993). The extremely sandy nature of the soil in the present study may preclude large differences in soil moisture between pit and mound. Peterson & Pickett (1990) proposed that such moisture differences are primary determinants of species composition in tipup mound microsites.

Peterson & Pickett (1995) observed convergence of species assemblages in forest and blowdown areas within 7-8 yr after a tornado. Unfortunately, there are no intact pine forests in the vicinity, so we are not able to make a comparison. However, as evidenced by the CCA (Fig. 1), species composition is not (yet) returning to pre-disturbance conditions.

The intact forest floor seemed to be quite resistant to invasion by the ruderal species, (only once did any of the weedy species have > 10% frequency). Many of the existing

forest floor species in these plots appeared to respond favorably to the new regime, particularly *Maianthemum canadense*, *Anemone quinquefolia* and *Arisaema triphyllum*. Thus they are tolerant of higher light, perhaps somewhat limited by light in the intact forest, and seemed to spread readily, after several years, to the other microsites.

The initial differences among the four microsite types have converged such that the current ground layer, while mounded and pitted, is remarkably similar in species composition. However, the forest floor has not returned to what it was, nor is it likely to, since the post-disturbance canopy will be likely dominated by hardwood species rather than pines (Arévalo et al. this volume). Accelerated canopy succession after a windstorm was found also by Dyer & Baird (1997) in other Minnesota forests. In the present study, the main differences from the predisturbance understory vegetation are a high frequency of *Polygonum cilinode* and *Dryopteris carthusiana*. We will continue to follow this forest to determine whether species composition on the different microsites will continue to converge through time, or diverge again.

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References

- Beatty, S.W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understorey plants. *Ecology* 65: 1406-1419.
- Carlton, G.C. & Bazzaz, F.A. 1998a. Resource congruence and forest regeneration following an experimental hurricane blowdown. *Ecology* 79: 1305-1319.
- Carlton, G.C. & Bazzaz, F.A. 1998b. Regeneration of three sympatric birch species on experimental hurricane blowdown microsites. *Ecol. Monogr.* 68: 99-120.
- Cornett, M.W., Reich, P.B. & Puettmann, K.J. 1997. Canopy feedbacks and microtopography regulate conifer seedling distribution in two Minnesota conifer-deciduous forests. *Écoscience* 4: 353-364.
- Denslow, J.S., Ellison, A.M. & Sanford, R.E. 1998. Treefall gap size effects on above- and below-ground processes in a tropical wet forest. *J. Ecol.* 86: 597-609.
- Ellison, A.M., Denslow, J.S., Loiselle, B.A. & Brenés, D.M. 1993. Seed and seedling ecology of Neotropical Melastomataceae. *Ecology* 74: 1733-1749.
- Jonsson, B. & Esseen, P. 1990. Treefall disturbance maintains high bryophyte diversity in a boreal spruce forest. *J. Ecol.* 78: 924-936.
- Kartesz, J.T. 1994. *A synonymized checklist of the vascular flora of the United States, Canada and Greenland. 2nd ed. Vol. 1 & 2.* Timber Press, Portland, OR.
- Nakashizuka, T. 1989. Role of uprooting in composition and dynamics of an old-growth forest in Japan. *Ecology* 70: 1273-1278.
- Núñez-Farfán, J. & Dirzo, R. 1998. Within gap spatial heterogeneity and seedling performance in a Mexican tropical forest. *Oikos* 51: 274-284.
- Peterson, C.J. & Campbell, J.E. 1993. Microsite differences and temporal change in plant communities of treefall pits and mounds in an old-growth forest. *Bull. Torr. Bot. Club* 120: 451-460.
- Peterson, C.J. & Carson, W.P. 1996. Generalizing forest regeneration models: the dependence of propagule availability on disturbance history and stand size. *Can. J. For. Res.* 26: 45-52.
- Peterson, C.J. & Pickett, S.T.A. 1990. Microsite and elevational influences on early forest regeneration after catastrophic windthrow. *J. Veg. Sci.* 1: 657-662.
- Peterson, C.J. & Pickett, S.T.A. 1991. Treefall and resprouting following catastrophic windthrow in an old-growth hemlock-hardwoods forest. *For. Ecol. Manage.* 42: 205-217.
- Peterson, C.J. & Pickett, S.T.A. 1995. Forest reorganization: a case study in an old-growth catastrophic blowdown. *Ecology* 76: 763-774.
- Peterson, C.J., Carson, W.P., McCarthy, B.C. & Pickett, S.T.A. 1990. Microsite variation and soil dynamics within newly created treefall pits and mounds. *Oikos* 58: 39-46.
- Putz, F.E. 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer tree species on Barro Colorado Island, Panama. *Ecology* 64: 1069-1074.
- Schaetzl, R.J., Burns, S.F., Johnson, D.L. & Small, T.W. 1989a. Tree uprooting: review of impacts on forest ecology. *Vegetatio* 79: 165-176.
- Schaetzl, R.J., Johnson, D.L., Burns, S.F. & Small, T.W. 1989b. Tree uprooting: review of terminology, process and environmental implications. *Can. J. For. Res.* 19: 1-11.
- ter Braak, C.J.F. 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. *Vegetatio* 69: 69-77.
- ter Braak, C.J.F. & Šmilauer, P. 1998. *CANOCO Reference Manual and User's Guide for Canoco for Windows: Software for Canonical Community Ordination (version 4).* Microcomputer Power, Ithaca, NY.
- Thompson, J.H. 1980. Treefalls and colonization patterns of temperate forest herbs. *Am. Midl. Nat.* 104: 176-184.
- Webb, S.L. 1988. Windstorm damage and microsite colonization in two Minnesota forests. *Can. J. For. Manage.* 18: 1186-1195.