

The effects of disturbance intensity on temporal and spatial patterns of herb colonization in a southern New England mixed-oak forest

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Abstract

As managing forests for biodiversity becomes more common, it is important to understand how understory species respond to disturbance. We monitored changes in species' dominance, calculated as importance values, over a 4-year period in order to determine how species' dominance varied with disturbance intensity and gap position. An experimental linear canopy opening was created in a southern New England mixed-oak forest, and plots were established on the south side, center, and north side of the opening. All vegetation was removed in half of the plots, simulating a lethal disturbance. In the other half of the plots, only the overstory was removed, simulating minimal disturbance (release plot). Before the disturbance, *Dennstaedtia punctilobula* dominated the plots, but typical forest understory species such as *Kalmia latifolia*, *Trientalis borealis*, *Maianthemum canadense*, and *Mitchella repens* were very common. After the disturbance, *D. punctilobula* expanded and continued to remain dominant in all types of plots. Early successional species, such as *Carex pensylvanica*, Poaceae species, *Rubus ideaus*, and *Rubus allegheniensis* dominated the lethal and center plots; late successional forest understory species experienced a reduction in frequency and cover in these plots. However, in release and edge plots, late successional species maintained relatively similar frequencies and covers to pre-disturbance values. The ability of early successional species to seed into lethal plots and grow rapidly in the high light environment of the center plots allowed them to dominate in these plots. Late successional species were able to remain relatively dominant in release plots through clonal expansion and in edge plots through exclusion of early successional species from low light levels. Three years after the disturbance, most of the residual forest understory species had attained similar frequencies and covers to pre-disturbance values in all types of plots. Thus, although there is some initial loss of residual species in highly disturbed areas and in the center of the opening, most of these species are able to recover in a relatively short time period. However, locally uncommon species may be vulnerable to permanent loss. In order to minimize loss of species from the understory, forest managers should attempt to keep groundstorey disturbance as minimal as possible where desirable late-successional species exist and create edge-partial shade effects with the remaining canopy for regeneration treatments.

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1. Introduction

Traditionally, studies examining the effects of silvicultural treatments on regeneration have focused on commercially valuable tree species rather than the shrub and herb species that comprise the understory stratum. However, these species play an important, though often overlooked, role in the forest ecosystem. Several studies have found that certain herbs and shrubs shape forest development through competition with tree

seedlings (Horsley and Marquis, 1983; Maguire and Forman, 1983; Berkowitz et al., 1995; Beckage et al., 2000). Reduced light levels and increased seed predation under the herbaceous layer result in differential species establishment and survival, influencing the spatial patterns of tree species (George and Bazzaz, 1999a,b; de la Cretaz and Kelty, 2002; George and Bazzaz, 2003).

Additionally, the herbaceous layer is the most diverse stratum in eastern deciduous forests (Gilliam and Roberts, 2003), contributing significantly to the biodiversity of the ecosystem. Biodiversity is valued for both ecological and economical reasons. It promotes the ecological health and stability of a system while providing an array of species that are

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increasingly being recognized for their economic value as food or medicinal resources (Burton et al., 1992). With the recent emphasis on including biodiversity as a forest management objective (Burton et al., 1992; Roberts and Gilliam, 1995), there is a need to understand how the understory stratum and the species that inhabit it respond to and recover from disturbance.

Many studies have used species' life history characteristics to explain responses to disturbance (Sousa, 1980; Pickett, 1982; Hobbs et al., 1984; McIntyre et al., 1995), and predictive models of succession have been created which incorporate these traits (Drury and Nisbet, 1973; Grime, 1979; Cattelino et al., 1979; Noble and Slatyer, 1980). Reproductive strategy and stress tolerance from competition are important factors in the species' establishment, and life history traits such as growth rate, carbon allocation, and life span determine patterns of species abundance over time.

Although temporal patterns of succession have been studied extensively (Halpern, 1988; Fredericksen et al., 1999; Battles et al., 2001), spatial patterns of species abundance have been studied much less. In temperate latitudes, canopy openings created by disturbances have a heterogeneous light environment. The angle of the sun causes light to hit the gap floor at an angle rather than from directly overhead. In northern temperate latitudes, this results in higher light at the north edge than the south edge of the opening (Geiger, 1965; Poulson and Platt, 1989; Canham et al., 1990).

Investigations of patterns of herbaceous species composition and abundance in response to gap position have not yielded consistent results. Collins and Pickett (1988) found significant differences in early summer herb and fern cover in different gap positions at some, but not all, sites. Further studies are needed to determine how understory species respond to the gap microenvironment.

The objective of this study was to examine temporal and spatial patterns of understory species abundance in relation to both disturbance intensity and canopy opening position during early succession. Response of species to two disturbance intensities was measured: a lethal treatment in which all plants in the understory were removed and a release treatment in which the understory remained intact. In addition, plots were located in one of three positions: the north edge, the south edge, or the center of the canopy opening. Resulting patterns of

species abundance were examined in the context of a subset of species' life history characteristics.

Based on previous literature, we predicted that lethal plots will be dominated by shade-intolerant, early successional species reproducing from buried or wind-dispersed seed, whereas release plots will be dominated by clonally-reproducing individuals that survived the disturbance. We also predicted that shade-intolerant, early successional species will be found more often in center and north plots, and shade-tolerant forest understory species will be observed more often in south plots. Lastly, we predicted that post-disturbance release plots and southern edge and understory plots will have a composition most similar to pre-disturbance flora, whereas lethal, center, and northern edge plots will have a composition least like the pre-disturbance flora.

2. Methods

2.1. Study site

The experiment was conducted at the Yale-Myers forest in northeastern Connecticut, USA (41°57'N, 72°07'W). Yale-Myers is comprised of 3160 ha of mixed deciduous second-growth forest arising from agricultural land abandonment in the nineteenth century (Meyer and Plusnin, 1945). The topography is characterized by undulating hills with broad ridges and narrow valleys. The elevation ranges from a low of 170 m above sea level to a high point of 300 m above sea level. Soils are glacial tills made up of moderate to well-drained stony loams overlying metamorphic bedrock (Ashton and Larson, 1996).

The climate is characterized as cool temperate and humid. Mean annual summer temperature is 20 °C, and mean annual winter temperature is -4 °C. Precipitation is evenly distributed throughout the year with a mean of 110 cm (Ashton and Larson, 1996).

The study site is located in a mid-slope 85-year-old stand with a northerly aspect (Ashton et al., 1998). The height of the canopy is 50 feet, and the angle of the slope is 7% to the northwest. Prior to the creation of the gap, the stand was dominated by *Quercus rubra* (northern red oak) in the canopy and *Acer rubrum* (red maple) and *Betula lenta* (black birch) in the subcanopy and understory (Table 1). Total density was 376.54 stems/ha, and total basal area was 15.09 m²/ha.

Table 1
Mean diameter breast height (DBH), density, and basal area by species of the study site before gap creation

Species		Mean DBH (cm)	Density (stems/ha)	BA (m ² /ha)
<i>Acer rubrum</i> L.	Red maple	15.63	111.11	2.46
<i>Acer saccharum</i> Marsh.	Sugar maple	8.68	37.04	0.26
<i>Betula lenta</i> L.	Black birch	14.22	77.16	1.52
<i>Betula papyrifera</i> Marsh.	Paper birch	27.94	9.26	0.58
<i>Fagus grandifolia</i> Ehrh.	American beech	10.16	3.09	0.03
<i>Pinus strobus</i> L.	White pine	22.86	9.26	0.48
<i>Prunus serotina</i> Ehrh.	Black cherry	10.16	3.09	0.03
<i>Quercus rubra</i> L.	Northern red oak	31.41	92.59	8.03
<i>Tsuga canadensis</i> (L.) Carr.	Eastern hemlock	23.55	33.95	1.71
Total			376.54	15.09

2.2. Experimental design

During the summer of 1999, we delineated a 108 m × 30 m rectangular area, oriented east-west lengthwise, as a future gap in the study site. Within this area, we created four parallel rows of eight plots in the east-west direction, comprised of two center rows and two edge rows. In addition, we created two parallel understory rows of eight plots each in an east-west direction outside of the delineated area, one row located 20 m to the north and one row located 20 m to the south of the future gap. Although there is variability in the distance light persists from an edge into the surrounding forest, several studies have found that light levels generally decline to typical understory levels within approximately 20 m from the edge (Matlack, 1993; Young and Mitchell, 1994).

We created a total of six rows and 48 plots. Each plot was 2 m × 2 m. We designated the plots as either lethal or release in a randomized block design.

In the winter of 2000, the delineated area was harvested with a Timbco feller-buncher (Timbco Hydraulics, Shawano, WI). Slash was piled in the center of the gap, between the two center rows. We treated the lethal plots with glyphosate herbicide (Roundup, Monsanto Corporation, St. Louis, MO) in early June 2000 and scarified the plots 2 weeks later. Scarification involved mixing the organic pad with the mineral soil. Only the top 10 cm of soil was disturbed, leaving the seed bank beneath intact. We did not treat the understory in release plots.

We constructed an electrical fence in the summer of 2000 around the perimeter of the study site, encompassing all plots to restrict access by deer. Each spring, we fixed the fence from damage suffered during the winter months.

2.3. Field sampling

We sampled once before the harvest in the summer of 1999, and again in the summers of 2001, 2002, and 2003. We only sampled once during early-summer (late June–early July; however, from frequent year round observations this site has no spring ephemerals that would not have been captured in the early summer sampling regime and there are no known fall ephemerals in this forest region. In each plot, we identified all herbaceous and shrubby species and recorded percent cover of each species on a six point scale according to Daubenmire (1959). Nomenclature of species follows Fernald (1970).

2.4. Life history characteristics

We characterized each species recorded during the sampling period according to its life cycle (annual, biennial, or perennial), reproductive strategy (clonal, buried seed, animal-dispersed seed, or wind-dispersed seed), whether or not it was evergreen, and its life form (herb, shrub, fern, or liana) (Table 2). Reproductive strategy was defined as the method of reproduction most likely used in colonization and expansion by a species at this particular site, based on pre-disturbance vegetation. Thus, species designated as clonal were present before the disturbance, and all species that arrived at the site

after the disturbance were classified with seed reproduction strategies. Species were deemed capable of buried seed germination if they had been found in buried seed bank studies (Oosting and Humphreys, 1940; Olmsted and Curtis, 1947; Livingston and Alessio, 1968; Graber and Thompson, 1978; Matlack and Good, 1990; Hughes and Fahey, 1991; Schiffman and Johnson, 1992; Ashton et al., 1998; Leckie et al., 2000). Dispersal strategies were based on previous studies (Beattie and Culver, 1981; Matlack, 1994; Cain et al., 1998; McLachlan and Bazely, 2001; Singleton et al., 2001; Bellemare et al., 2002). Several species' reproductive strategies were based on those of a congener (*Vitis labrusca* and *V. rotundifolia* (*V. aestivalis*), *Rubus flagellaris* and *R. occidentalis* (*Rubus ideaus* and *Rubus allegheniensis*), *Aralia hispida* (*A. nudicaulis*), and *Galium lanceolatum* (*G. aparine* and *G. trifolium*)). Characteristics of species identified only to genus were based on those common species of that genus found in the area.

2.5. Data analysis

We analyzed differences in percent cover of species with disturbance intensity, canopy opening position, and disturbance intensity × canopy opening position with MANOVA in SAS (PROC GLM, Version 8.2, SAS Institute, 2001) for pre-disturbance and post-disturbance time periods. Post-disturbance data was analyzed with a doubly-multivariate repeated measures design, using species and time as repeated measure factors. Wilks' Lambda values were used in all MANOVA tests. Species found in less than four plots each sampling year were lumped together as "rare" species. The highest cover class among the rare species present in a plot was used as the cover class of the rare species category for that particular plot.

We analyzed species composition differences between disturbance intensities and gap positions through detrended correspondence analysis (DCA), using percent cover of species, in PC-ORD (Version 4.17, McCune and Mefford, 1999). All species were used in the analyses, but rare species were downweighted. We used MANOVA (PROC GLM, SAS Version 8.2, SAS Institute, 2001) to test for differences in percent cover after the disturbance between different intensities and different canopy opening positions for annuals and biennials (lumped together), evergreen species, seed-reproducing species, and clonal species. Wilks' lambda values were used in all MANOVA tests. Species found in less than four plots were not included in the analyses.

We converted the cover class of each species in each plot to percent cover, using the median percent value of the cover class. We computed importance values for each species, calculated as relative frequency + relative percent cover. We did this for each type of disturbance intensity (lethal and release) and each canopy opening position (north, center, and south) for each year. Center plots included the two center rows. South plots included the edge and understory rows on the south side of the opening, and north plots included the edge and understory rows on the north side of the opening. Statistical analyses showed there were no significant differences in the

Table 2
Life history characteristics of the understory species observed during sampling

Species	Abbreviation	Life cycle	Reproductive strategy	Evergreen	Life form
<i>Amelanchier arborea</i> (Michx. f.) Fern.	AMAR	P	BS ⁸ /A	NE	S
<i>Amphicarpa bracteata</i> (L.) Fern.	AMBR	P	B	NE	H
<i>Anaphalis margaritacea</i> (L.) Benth. & Hook.	ANMA	B	W	NE	H
<i>Anemone quinquefolia</i> L.	ANQU	P	A	NE	H
<i>Aralia hispida</i> Vent.	ARHI	P	BS ^{3,4} /A	NE	H
<i>Aralia nudicaulis</i> L.	ARNU	P	C	NE	H
<i>Aster divaricatus</i> L.	ASDI	B	W	NE	H
<i>Carex pensylvanica</i> Lam.	CAPE	P	C	NE	H
<i>Chimaphila maculata</i> (L.) Pursh.	CHMA	P	C	E	H
<i>Cimicifuga racemosa</i> (L.) Nutt.	CIRA	P	N	NE	H
<i>Dennstaedtia punctilobula</i> (Michx.) Moore	DEPU	P	C	NE	F
<i>Duchesnea indica</i> (Andr.) Focke	DUIN	P	A	E	H
<i>Erechtites hieracifolia</i> (L.) Raf.	ERHI	A	BS ^{1,3,5} /W	NE	H
<i>Galium boreale</i> L.	GABO	P	BS ^{1,2} /A	NE	H
<i>Galium lanceolatum</i> Torr.	GALA	P	BS ^{1,2} /A	NE	H
<i>Gaultheria procumbens</i> L.	GAPR	P	C	E	H
<i>Houstonia caerulea</i> L.	HOCA	P	N	NE	H
<i>Juncus</i> spp.	JUNX	P	BS ^{3,5} /W	NE	H
<i>Kalmia latifolia</i> L.	KALA	P	C	E	S
<i>Lactuca canadensis</i> L.	LACA	A	W	NE	H
<i>Lobelia inflata</i> L.	LOIN	A	N	NE	H
<i>Lycopodium annotinum</i> L.	LYAN	P	C	E	F
<i>Lycopodium complanatum</i> L.	LYCO	P	S	E	F
<i>Lycopodium obscurum</i> L.	LYOB	P	C	E	F
<i>Lycopodium lucidulum</i> Michx.	LYLU	P	W	E	F
<i>Lysimachia quadrifolia</i> Sims	LYQU	P	N	NE	H
<i>Maianthemum canadense</i> Desf.	MACA	P	C	NE	H
<i>Medeola virginiana</i> L.	MEVI	P	C	NE	H
<i>Melampyrum lineare</i> Desr.	MELI	A	N	NE	H
<i>Mitchella repens</i> L.	MIRE	P	C	E	H
<i>Monotropa uniflora</i> L.	MOUN	P	N	NE	H
<i>Phytolacca americana</i> L.	PHAM	P	BS ^{3,5,7} /A	NE	H
Poaceae	POAX	A/P	BS ^{3,6,8} /W	NE	H
<i>Polygonatum biflorum</i> (Walt.) Ell.	POBI	P	A	NE	H
<i>Polystichum acrostichoides</i> (Michx.) Schott	POAC	P	C	E	F
<i>Potentilla simplex</i> Michx.	POSI	A/B	BS ^{3,8,9} /N	NE	H
<i>Rhus copallinum</i> L.	RHCO	P	BS ¹ /A	NE	S
<i>Rubus allegheniensis</i> Porter	RUAL	P	BS ^{3,6,8} /A	NE	S
<i>Rubus flagellaris</i> L.	RUFL	P	BS/A	NE	S
<i>Rubus idaeus</i> L.	RUID	P	C/BS ^{3,6,8} /A	NE	S
<i>Rubus occidentalis</i> L.	RUOC	P	BS/A	NE	S
<i>Rudbeckia serotina</i> Farw.	RUSE	B	W	NE	H
<i>Solidago canadensis</i> L.	SOCA	P	BS ^{1,3,4} /W	NE	H
<i>Solidago rugosa</i> P. Mill	SORU	P	BS ^{1,3,4} /W	NE	H
<i>Thelypteris novaboracensis</i> (L.) Nieuwl.	THNO	P	W	NE	F
<i>Trientalis borealis</i> Raf.	TRBO	P	C	NE	H
<i>Trifolium pratense</i> L.	TRPR	B	BS ^{1,3} /W	NE	H
<i>Uvularia sessilifolia</i> L.	UVSE	P	BS ^{4,6} /A	NE	H
<i>Vaccinium angustifolium</i> Ait.	VAAN	P	C	NE	S
<i>Vaccinium corymbosum</i> L.	VACO	P	A	NE	S
<i>Vaccinium vacillans</i> Torr.	VAVA	P	C	NE	S
<i>Verbascum thapsus</i> L.	VETH	B	BS ^{3,7,8} /W	NE	H
<i>Viola sororia</i> Wild.	VISO	P	C	NE	H
<i>Vitis labrusca</i> L.	VILA	P	BS ⁸ /A	NE	L
<i>Vitis rotundifolia</i> Michx.	VIRO	P	BS ⁸ /A	NE	L

Abbreviations are as follows: Life Cycle: A, annual; B, biennial; P, perennial; Reproductive Strategy: C, clonal; BS, buried seed; A, animal dispersed; B, ballistic dispersed; W, wind dispersed; N, no dispersal mechanism identified; Evergreen: NE, nonevergreen; E, evergreen; Life Form: F, ferns and Allies; H, herb; L, liana; S, shrub.

References: ¹Oosting and Humphreys (1940), ²Olmsted and Curtis (1947), ³Livingston and Alessio (1968), ⁴Graber and Thompson (1978), ⁵Matlack and Good (1990), ⁶Hughes and Fahey (1991), ⁷Schiffman and Johnson (1992), ⁸Ashton et al. (1998), ⁹Leckie et al. (2000).

edge and understory plots for both the north and south sides, allowing us to lump them together.

We analyzed temporal trends in early succession for disturbance intensity and canopy opening position through DCA, using species' importance values, in PC-ORD (Version 4.12, McCune and Mefford, 1999). All species were used in the analyses, but rare species were downweighted.

3. Results

3.1. Disturbance intensity: species composition

Prior to the creation of the experimental linear canopy opening, 18 species were observed in the plots. Percent cover of species did not differ significantly between the two types of disturbance plots (MANOVA, $F = 0.94$, d.f. = 9, 34, $P = 0.5035$), indicating similar species composition. *Dennstaedtia punctilobula* dominated both the lethal and release plots (Table 3).

In the 3 years following the disturbance, percent cover of species was significantly different between lethal and release plots (MANOVA, $F = 6.25$, d.f. = 34, 9, $P = 0.0033$). Ordination through DCA, based on species' percent covers, revealed differences in species composition between the two intensities for all three post-disturbance years. Temporal trends, based on species' importance values, showed that although species composition changed after both types of disturbances, release plots had a more similar species composition to pre-disturbance plots (Fig. 1). The year after the disturbance showed the greatest difference between the two intensities. However, as the years progressed, the species composition of both intensities began to return to pre-disturbance composition, becoming more similar.

Although the species composition of lethal and release plots was different 1 year after the disturbance, *D. punctilobula* and *Carex pensylvanica* continued to remain the dominant species in both plots (Table 3). Whereas only a few species dominated the release plots, many species shared similar importance values in the lethal plots. Several new species became quite common in lethal plots, including *Rubus idaeus*, *Lysimachia quadrifolia*, *Erechtites hieracifolia*, and *V. labrusca*.

Three of the most dominant species in 1999, *Kalmia latifolia*, *Trientalis borealis* and *Maianthemum canadense*, significantly decreased in frequency, average percent cover, and importance value after the disturbance (see Table 3). Whereas *T. borealis* decreased in all respects by about the same amount in lethal and release plots, *K. latifolia* and *M. canadense* showed a more dramatic decrease in the lethal plots than release plots.

Three years after the disturbance, *D. punctilobula* continued to be the dominant species in both release and lethal plots, followed by *C. pensylvanica* (Table 3). However, besides those two species, lethal and release plots were dominated by different suites of species. Lethal plots contained *L. quadrifolia*, Poaceae species, *R. allegheniensis*, and *T. borealis*, whereas release plots were dominated by *K. latifolia*, *M. canadense*, *R. allegheniensis*, and *T. borealis*.

3.2. Disturbance intensity: life-history characteristics

There were no annuals or biennials in the plots before the disturbance, and thus, statistical tests for differences of annual and biennial species between disturbance intensities in 1999 could not be done. In the years after the disturbance, several annuals and biennials colonized both lethal and release plots. MANOVA on percent cover of annuals and biennials showed that lethal and release plots had significantly different percent covers of annual and biennial species ($F = 3.19$, d.f. = 7, 36, $P = 0.0098$).

The first year after the disturbance had the greatest disparity in numbers of annuals/biennials between the two intensities with lethal plots containing eight species and release plots containing only three species. However, by 2003, there were equal numbers of annuals/biennials in each type of disturbance plot.

Before the disturbance, seven evergreen species were present in the plots. There were no differences in percent covers of common evergreen species between the two disturbance plot types (MANOVA, $F = 1.59$, d.f. = 2, 41, $P = 0.2171$).

MANOVA indicated significant differences in percent covers of evergreen species between lethal and release plots ($F = 2.88$, d.f. = 4, 39, $P = 0.0350$) in the 3 years after disturbance. Evergreen species were initially negatively impacted by the lethal disturbance. In the year after the disturbance, *Chimaphila maculata*, *Gaultheria procumbens*, *Polystichum acrostichoides*, and *Lycopodium annotinum* disappeared from the plots. Additionally, *K. latifolia* significantly decreased in frequency and average percent cover, and *Mitchella repens* decreased slightly in frequency in lethal plots. However, after the initial decreases in lethal plots, all evergreen species either increased or maintained approximately the same frequencies and percent covers in the years since 2001. The evergreen species were generally more dominant in release than lethal plots (see Table 3).

Before the disturbance, only one species was present in the plots that reproduced solely through sexual reproduction. Thus, statistical tests for differences with disturbance intensity and gap position before the disturbance were not conducted with reproductive strategy. After the disturbance, there were significant differences in percent covers of seed reproducing species between lethal and release plots (MANOVA, $F = 2.65$, d.f. = 23, 20, $P = 0.0157$). Differences were also found between disturbance intensities for percent covers of clonal species (MANOVA, $F = 3.15$, d.f. = 11, 32, $P = 0.0055$).

Generally, species that reproduced by seed were more abundant in lethal plots, whereas clonal species were more abundant in release plots. Of the eight most dominant species in each disturbance plot in 2001, six species in the release plots reproduced clonally compared to only three in the lethal plots. Four species found in lethal plots in 2001 were capable of germinating from seed banks.

3.3. Canopy opening position

Before the creation of the canopy opening, the center and north plots had a similar number of species, but the south plots

Table 3

Frequency (a), average percent cover (b) and importance values (c) of all species found in lethal and release treatments before the treatment, 1 year after the treatment, and 3 years after the treatment

Species	Lethal			Release		
	Before	1 Year after	3 Years after	Before	1 Year after	3 Years after
(a) Frequency						
AMAR	0.0	0.0	0.0	0.0	4.2	0.0
AMBR	0.0	0.0	0.0	4.2	0.0	0.0
ANMA	0.0	4.2	0.0	0.0	0.0	0.0
ANQU	0.0	0.0	0.0	0.0	0.0	4.2
ARHI	0.0	0.0	16.7	0.0	0.0	12.5
ARNU	4.2	0.0	0.0	4.2	16.7	25.0
ASDI	0.0	4.2	4.2	0.0	16.7	12.5
CAPE	50.0	83.3	91.7	58.3	79.2	95.8
CHMA	4.2	0.0	0.0	0.0	0.0	0.0
CIRA	0.0	0.0	0.0	0.0	8.3	0.0
DEPU	45.8	45.8	62.5	58.3	62.5	79.2
DUIN	0.0	8.3	0.0	0.0	4.2	0.0
ERHI	0.0	25.0	4.2	0.0	16.7	0.0
GABO	0.0	0.0	8.3	0.0	0.0	0.0
GALA	0.0	8.3	0.0	0.0	16.7	0.0
GAPR	4.2	0.0	0.0	0.0	0.0	0.0
HOCA	0.0	0.0	25.0	0.0	0.0	4.2
JUNX	0.0	4.2	0.0	0.0	0.0	0.0
KALA	25.0	4.2	12.5	37.5	33.3	37.5
LACA	0.0	0.0	0.0	0.0	0.0	4.2
LOIN	0.0	4.2	0.0	0.0	0.0	0.0
LYAN	8.3	0.0	0.0	4.2	0.0	0.0
LYOB	4.2	4.2	4.2	0.0	4.2	0.0
LYLU	0.0	0.0	8.3	0.0	0.0	16.7
LYQU	0.0	37.5	58.3	0.0	4.2	29.2
MACA	41.7	4.2	50.0	45.8	20.8	70.8
MEVI	0.0	0.0	0.0	4.2	0.0	8.3
MELI	0.0	0.0	20.8	0.0	0.0	16.7
MIRE	29.2	25.0	37.5	45.8	54.2	54.2
MOUN	0.0	0.0	0.0	0.0	8.3	4.2
PHAM	0.0	16.7	8.3	0.0	8.3	4.2
POAX	0.0	41.7	79.2	0.0	12.5	29.2
POBI	0.0	0.0	0.0	0.0	0.0	8.3
POAC	0.0	0.0	0.0	4.2	0.0	0.0
POSI	0.0	8.3	41.7	0.0	0.0	16.7
RHCO	0.0	4.2	4.2	0.0	0.0	0.0
RUAL	0.0	0.0	70.8	0.0	0.0	33.3
RUFL	0.0	12.5	4.2	0.0	4.2	8.3
RUID	0.0	45.8	8.3	4.2	25.0	20.8
RUOC	0.0	0.0	12.5	0.0	0.0	29.2
RUSE	0.0	0.0	16.7	0.0	0.0	4.2
SOCA	0.0	0.0	8.3	0.0	0.0	0.0
SORU	0.0	4.2	8.3	0.0	0.0	8.3
THNO	0.0	0.0	8.3	0.0	0.0	20.8
TRBO	66.7	12.5	75.0	75.0	20.8	100.0
TRPR	0.0	4.2	0.0	0.0	0.0	0.0
UVSE	0.0	0.0	16.7	0.0	4.2	20.8
VAAN	25.0	4.2	37.5	16.7	12.5	25.0
VACO	0.0	20.8	0.0	0.0	25.0	0.0
VAVA	8.3	0.0	0.0	0.0	0.0	0.0
VETH	0.0	4.2	0.0	0.0	0.0	0.0
VISO	4.2	45.8	37.5	12.5	8.3	16.7
VILA	0.0	37.5	12.5	0.0	16.7	4.2
VIRO	0.0	0.0	12.5	0.0	0.0	8.3
(b) Average percent cover						
AMAR	0.0	0.0	0.0	0.0	0.1	0.0
AMBR	0.0	0.0	0.0	0.1	0.0	0.0
ANMA	0.0	0.1	0.0	0.0	0.0	0.0
ANQU	0.0	0.0	0.0	0.0	0.0	0.1
ARHI	0.0	0.0	0.4	0.0	0.0	0.3

Table 3 (Continued)

Species	Lethal			Release		
	Before	1 Year after	3 Years after	Before	1 Year after	3 Years after
ARNU	0.1	0.0	0.0	0.1	0.4	0.6
ASDI	0.0	0.1	0.1	0.0	0.4	0.3
CAPE	1.3	5.2	11.8	1.5	6.7	17.9
CHMA	0.1	0.0	0.0	0.0	0.0	0.0
CIRA	0.0	0.0	0.0	0.0	0.2	0.0
DEPU	9.6	5.2	14.9	10.9	16.1	38.6
DUIN	0.0	0.7	0.0	0.0	0.1	0.0
ERHI	0.0	1.7	0.1	0.0	0.4	0.0
GABO	0.0	0.0	0.2	0.0	0.0	0.0
GALA	0.0	0.2	0.0	0.0	0.4	0.0
GAPR	0.1	0.0	0.0	0.0	0.0	0.0
HOCA	0.0	0.0	0.6	0.0	0.0	0.1
JUNX	0.0	0.1	0.0	0.0	0.0	0.0
KALA	5.1	0.6	0.3	10.8	5.3	10.8
LACA	0.0	0.0	0.0	0.0	0.0	0.1
LOIN	0.0	0.1	0.0	0.0	0.0	0.0
LYAN	0.7	0.0	0.0	0.1	0.0	0.0
LYOB	0.1	0.1	0.1	0.0	0.1	0.0
LYLU	0.0	0.0	0.2	0.0	0.0	0.4
LYQU	0.0	2.0	3.0	0.0	0.1	0.7
MACA	1.0	0.1	1.3	1.1	0.5	1.8
MEVI	0.0	0.0	0.0	0.1	0.0	0.2
MELI	0.0	0.0	0.5	0.0	0.0	0.4
MIRE	0.7	0.6	0.9	1.1	1.9	1.4
MOUN	0.0	0.0	0.0	0.0	0.2	0.1
PHAM	0.0	0.4	0.2	0.0	0.2	0.1
POAX	0.0	2.1	4.6	0.0	0.3	1.3
POBI	0.0	0.0	0.0	0.0	0.0	0.2
POAC	0.0	0.0	0.0	0.1	0.0	0.0
POST	0.0	0.2	2.6	0.0	0.0	0.4
RHCO	0.0	0.1	0.1	0.0	0.0	0.0
RUAL	0.0	0.0	10.7	0.0	0.0	6.4
RUFL	0.0	0.3	0.1	0.0	0.1	0.2
RUID	0.0	1.7	0.2	0.1	1.1	0.5
RUOC	0.0	0.0	0.3	0.0	0.0	1.8
RUSE	0.0	0.0	0.4	0.0	0.0	0.1
SOCA	0.0	0.0	0.2	0.0	0.0	0.0
SORU	0.0	0.1	0.2	0.0	0.0	0.2
THNO	0.0	0.0	0.2	0.0	0.0	0.5
TRBO	1.7	0.3	1.9	1.9	0.5	2.5
TRPR	0.0	0.1	0.0	0.0	0.0	0.0
UVSE	0.0	0.0	0.4	0.0	0.1	0.5
VAAN	0.6	0.1	0.9	0.4	0.8	2.6
VACO	0.0	0.5	0.0	0.0	1.1	0.0
VAVA	0.2	0.0	0.0	0.0	0.0	0.0
VETH	0.0	0.1	0.0	0.0	0.0	0.0
VISO	0.1	1.1	0.9	0.3	0.2	0.4
VILA	0.0	0.9	0.3	0.0	0.4	0.1
VIRO	0.0	0.0	0.3	0.0	0.0	0.2
(c) Importance value						
AMAR	0.0	0.0	0.0	0.0	1.1	0.0
AMBR	0.0	0.0	0.0	1.5	0.0	0.0
ANMA	0.0	1.2	0.0	0.0	0.0	0.0
ANQU	0.0	0.0	0.0	0.0	0.0	0.6
ARHI	0.0	0.0	2.6	0.0	0.0	1.8
ARNU	1.8	0.0	0.0	1.5	4.5	3.7
ASDI	0.0	1.2	0.7	0.0	4.5	1.8
CAPE	21.4	36.7	30.5	20.6	33.8	31.0
CHMA	1.8	0.0	0.0	0.0	0.0	0.0
CIRA	0.0	0.0	0.0	0.0	2.3	0.0
DEPU	58.9	29.6	32.4	53.6	55.3	51.5
DUIN	0.0	4.5	0.0	0.0	1.1	0.0
ERHI	0.0	11.4	0.7	0.0	4.5	0.0

Table 3 (Continued)

Species	Lethal			Release		
	Before	1 Year after	3 Years after	Before	1 Year after	3 Years after
GABO	0.0	0.0	1.3	0.0	0.0	0.0
GALA	0.0	2.4	0.0	0.0	4.5	0.0
GAPR	1.8	0.0	0.0	0.0	0.0	0.0
HOCA	0.0	0.0	3.9	0.0	0.0	0.6
JUNX	0.0	1.2	0.0	0.0	0.0	0.0
KALA	31.6	3.3	2.0	47.7	20.8	16.3
LACA	0.0	0.0	0.0	0.0	0.0	0.6
LOIN	0.0	1.2	0.0	0.0	0.0	0.0
LYAN	6.0	0.0	0.0	1.5	0.0	0.0
LYOB	1.8	1.2	0.7	0.0	1.1	0.0
LYLU	0.0	0.0	1.3	0.0	0.0	2.5
LYQU	0.0	15.1	11.8	0.0	1.1	4.3
MACA	17.8	1.2	7.9	16.2	5.6	10.4
MEVI	0.0	0.0	0.0	1.5	0.0	1.2
MELI	0.0	0.0	3.3	0.0	0.0	2.5
MIRE	12.5	7.3	5.9	16.2	16.0	8.0
MOUN	0.0	0.0	0.0	0.0	2.3	0.6
PHAM	0.0	4.8	1.3	0.0	2.3	0.6
POAX	0.0	16.3	16.9	0.0	3.4	4.9
POBI	0.0	0.0	0.0	0.0	0.0	1.2
POAC	0.0	0.0	0.0	1.5	0.0	0.0
POSI	0.0	2.4	9.2	0.0	0.0	2.5
RHCO	0.0	1.2	0.7	0.0	0.0	0.0
RUAL	0.0	0.0	26.3	0.0	0.0	10.9
RUFL	0.0	3.6	0.7	0.0	1.1	1.2
RUID	0.0	15.4	1.3	1.5	8.1	3.1
RUOC	0.0	0.0	2.0	0.0	0.0	5.4
RUSE	0.0	0.0	2.6	0.0	0.0	0.6
SOCA	0.0	0.0	1.3	0.0	0.0	0.0
SORU	0.0	1.2	1.3	0.0	0.0	1.2
THNO	0.0	0.0	1.3	0.0	0.0	3.1
TRBO	28.5	3.6	11.8	26.5	5.6	14.7
TRPR	0.0	1.2	0.0	0.0	0.0	0.0
UVSE	0.0	0.0	2.6	0.0	1.1	3.1
VAAN	10.7	1.2	5.9	5.9	4.8	5.8
VACO	0.0	6.1	0.0	0.0	8.1	0.0
VAVA	3.6	0.0	0.0	0.0	0.0	0.0
VETH	0.0	1.2	0.0	0.0	0.0	0.0
VISO	1.8	13.3	5.9	4.4	2.3	2.5
VILA	0.0	10.9	2.0	0.0	4.5	0.6
VIRO	0.0	0.0	2.0	0.0	0.0	1.2

Importance value is calculated as relative frequency + relative average percent cover. Abbreviations used for the species are defined in Table 2.

had much fewer species (Table 4). *D. punctilobula* and *K. latifolia* dominated all canopy opening positions.

Species' percent cover did not differ significantly between canopy opening positions before the disturbance (MANOVA, $F = 1.17$, d.f. = 18, 68, $P = 0.3138$). However, six of the 18 species present had values that differed between the gap positions. *D. punctilobula* had a higher average percent cover in center plots, and *C. pensylvanica*, *K. latifolia*, *M. repens*, *T. borealis*, and *L. annotinum* had higher frequencies and percent covers in north plots.

After the disturbance, percent cover of species differed significantly between canopy opening positions (MANOVA, $F = 3.34$, d.f. = 68, 18, $P = 0.0030$). Contrasts showed that species percent cover differed significantly between the center of the opening and the north edge (MANOVA, $F = 6.08$, d.f. = 34, 9, $P = 0.0036$) and the center and the south edge

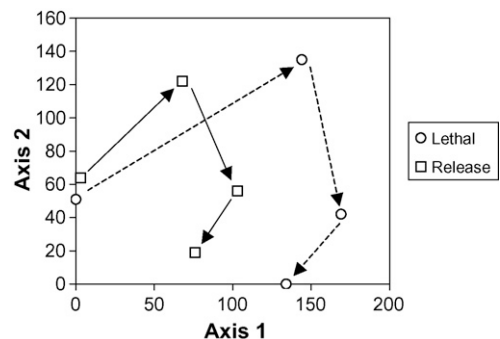


Fig. 1. Successional pathways over time of the different disturbance intensities (lethal vs. release) along the first two axes, using DCA ordination. Ordination was based on species' dominance. The first symbols for each pathway represent pre-disturbance species composition, and the arrows represent the pathway through successive years.

Table 4

Frequency (a), average percent cover (b) and importance values (c) of all species found in each canopy opening position before the treatment, 1 year after the treatment, and 3 years after the treatment

Species	Center			North			South		
	Before	1 Year after	3 Years after	Before	1 Year after	3 Years after	Before	1 Year after	3 Years after
(a) Frequency									
AMAR	0	0	0	0	0	0	0	6.3	0
AMBR	0	0	0	0	0	0	6.3	0	0
ANMA	0	6.3	0	0	0	0	0	0	0
ANQU	0	0	0	0	0	0	0	0	6.3
ARHI	0	0	25.0	0	0	6.3	0	0	12.5
ARNU	6.3	0	6.3	6.3	12.5	18.8	0	12.5	12.5
ASDI	0	0	0	0	12.5	18.8	0	18.8	6.3
CAPE	43.8	87.5	93.8	81.3	93.8	100.0	37.5	62.5	87.5
CHMA	6.3	0	0	0	0	0	0	0	0
CIRA	0	12.5	0	0	0	0	0	0	0
DEPU	56.3	68.8	87.5	50.0	50.0	56.3	50.0	43.8	68.8
DUIN	0	18.8	0	0	0	0	0	0	0
ERHI	0	43.8	6.3	0	12.5	0	0	6.3	0
GABO	0	0	6.3	0	0	6.3	0	0	0
GALA	0	18.8	0	0	18.8	0	0	0	0
GAPR	0	0	0	6.3	0	0	0	0	0
HOCA	0	0	12.5	0	0	12.5	0	0	18.8
JUNX	0	6.3	0	0	0	0	0	0	0
KALA	25.0	18.8	25.0	50.0	25.0	25.0	18.8	12.5	25.0
LACA	0	0	6.3	0	0	0	0	0	0
LOIN	0	6.3	0	0	0	0	0	0	0
LYAN	0	0	0	18.8	0	0	0	0	0
LYOB	0	0	0	6.3	12.5	0	0	0	6.3
LYLU	0	0	0	0	0	12.5	0	0	25.0
LYQU	0	31.3	62.5	0	18.8	56.3	0	12.5	12.5
MACA	50.0	6.3	43.8	43.8	18.8	62.5	37.5	12.5	75.0
MEVI	6.3	0	12.5	0	0	0	0	0	0
MELI	0	0	25.0	0	0	25.0	0	0	6.3
MIRE	18.8	18.8	25.0	62.5	62.5	75.0	31.3	37.5	37.5
MOUN	0	0	0	0	0	6.3	0	12.5	0
PHAM	0	37.5	18.8	0	0	0	0	0	0
POAX	0	43.8	68.8	0	31.3	75.0	0	6.3	18.8
POBI	0	0	12.5	0	0	0	0	0	0
POAC	6.3	0	0	0	0	0	0	0	0
POSI	0	6.3	56.3	0	6.3	25.0	0	0	6.3
RHCO	0	6.3	6.3	0	0	0	0	0	0
RUAL	0	0	87.5	0	0	37.5	0	0	6.3
RUFL	0	18.8	6.3	0	6.3	6.3	0	0	6.3
RUID	6.3	62.5	31.3	0	31.3	6.3	0	12.5	31.3
RUOC	0	0	56.3	0	0	6.3	0	0	0
RUSE	0	0	6.3	0	0	25.0	0	0	0
SOCA	0	0	6.3	0	0	6.3	0	0	0
SORU	0	6.3	18.8	0	0	6.3	0	0	0
THNO	0	0	12.5	0	0	25.0	0	0	6.3
TRBO	50.0	6.3	93.8	93.8	12.5	81.3	68.8	31.3	87.5
TRPR	0	6.3	0	0	0	0	0	0	0
UVSE	0	0	18.8	0	6.3	31.3	0	0	6.3
VAAN	18.8	0	25.0	25.0	12.5	37.5	18.8	12.5	31.3
VACO	0	31.3	0	0	31.3	0	0	6.3	0
VAVA	6.3	0	0	6.3	0	0	0	0	0
VETH	0	6.3	0	0	0	0	0	0	0
VISO	6.3	37.5	31.3	6.3	31.3	50.0	12.5	12.5	0
VILA	0	37.5	6.3	0	25.0	18.8	0	18.8	0
VIRO	0	0	18.8	0	0	6.3	0	0	6.3
(b) Average percent cover									
AMAR	0	0	0	0	0	0	0	0.2	0
AMBR	0	0	0	0	0	0	0.2	0	0
ANMA	0	0.2	0	0	0	0	0	0	0
ANQU	0	0	0	0	0	0	0	0	0.2
ARHI	0	0	0.6	0	0	0.2	0	0	0.3

Table 4 (Continued)

Species	Center			North			South		
	Before	1 Year after	3 Years after	Before	1 Year after	3 Years after	Before	1 Year after	3 Years after
ARNU	0.2	0	0.2	0.2	0.3	0.5	0	0.3	0.3
ASDI	0	0	0	0	0.3	0.5	0	0.5	0.2
CAPE	1.1	7.7	21.1	2.0	7.8	12.3	0.9	2.3	11.1
CHMA	0.2	0	0	0	0	0	0	0	0
CIRA	0	0.3	0	0	0	0	0	0	0
DEPU	14.1	17.5	43.8	8.8	6.6	16.9	8.0	8.0	19.7
DUIN	0	1.3	0	0	0	0	0	0	0
ERHI	0	2.7	0.2	0	0.3	0	0	0.2	0
GABO	0	0	0.2	0	0	0.2	0	0	0
GALA	0	0.5	0	0	0.5	0	0	0	0
GAPR	0	0	0	0.2	0	0	0	0	0
HOCA	0	0	0.3	0	0	0.3	0	0	0.5
JUNX	0	0.2	0	0	0	0	0	0	0
KALA	5.8	2.8	3.0	6.6	2.8	8.0	11.6	3.3	5.8
LACA	0	0	0.2	0	0	0	0	0	0
LOIN	0	0.2	0	0	0	0	0	0	0
LYAN	0	0	0	1.3	0	0	0	0	0
LYOB	0	0	0	0.2	0.3	0	0	0	0.2
LYLU	0	0	0	0	0	0.3	0	0	0.6
LYQU	0	1.6	3.1	0	1.3	2.2	0	0.3	0.3
MACA	1.3	0.2	1.1	1.1	0.5	1.6	0.9	0.3	1.9
MEVI	0.2	0	0.3	0	0	0	0	0	0
MELI	0	0	0.6	0	0	0.6	0	0	0.2
MIRE	0.5	0.5	0.6	1.6	2.3	1.9	0.8	0.9	0.9
MOUN	0	0	0	0	0	0.2	0	0.3	0
PHAM	0	0.9	0.5	0	0	0	0	0	0
POAX	0	1.9	4.1	0	1.6	3.4	0	0.2	1.3
POBI	0	0	0.3	0	0	0	0	0	0
POAC	0.2	0	0	0	0	0	0	0	0
POSI	0	0.2	3.8	0	0.2	0.6	0	0	0.2
RHCO	0	0.2	0.2	0	0	0	0	0	0
RUAL	0	0	22.3	0	0	2.5	0	0	0.2
RUFL	0	0.5	0.2	0	0.2	0.2	0	0	0.2
RUID	0.2	3.1	0.8	0	0.8	0.2	0	0.3	0.8
RUOC	0	0	3.0	0	0	0.2	0	0	0
RUSE	0	0	0.2	0	0	0.6	0	0	0
SOCA	0	0	0.2	0	0	0.2	0	0	0
SORU	0	0.2	0.5	0	0	0.2	0	0	0
THNO	0	0	0.3	0	0	0.6	0	0	0.2
TRBO	1.3	0.2	2.3	2.3	0.3	2.0	1.7	0.8	2.2
TRPR	0	0.2	0	0	0	0	0	0	0
UVSE	0	0	0.5	0	0.2	0.8	0	0	0.2
VAAN	0.5	0	0.6	0.6	1.1	3.9	0.5	0.3	0.8
VACO	0	0.8	0	0	1.6	0	0	0.2	0
VAVA	0.2	0	0	0.2	0	0	0	0	0
VETH	0	0.2	0	0	0	0	0	0	0
VISO	0.2	0.9	0.8	0.2	0.8	1.3	0.3	0.3	0
VILA	0	0.9	0.2	0	0.6	0.5	0	0.5	0
VIRO	0	0	0.5	0	0	0.2	0	0	0.2
(c) Importance value									
AMAR	0	0	0	0	0	0	0	2.7	0
AMBR	0	0	0	0	0	0	2.9	0	0
ANMA	0	1.3	0	0	0	0	0	0	0
ANQU	0	0	0	0	0	0	0	0	1.4
ARHI	0	0	3.0	0	0	0.9	0	0	2.7
ARNU	2.7	0	0.7	2.0	3.4	2.8	0	5.3	2.7
ASDI	0	0	0	0	3.4	2.8	0	8.0	1.4
CAPE	18.6	30.4	27.4	25.9	43.6	30.5	17.1	30.8	37.6
CHMA	2.7	0	0	0	0	0	0	0	0
CIRA	0	2.6	0	0	0	0	0	0	0
DEPU	73.6	49.2	46.3	46.0	31.2	33.0	49.9	54.8	52.4
DUIN	0	5.6	0	0	0	0	0	0	0
ERHI	0	12.6	0.7	0	3.4	0	0	2.7	0

Table 4 (Continued)

Species	Center			North			South		
	Before	1 Year after	3 Years after	Before	1 Year after	3 Years after	Before	1 Year after	3 Years after
GABO	0	0	0.7	0	0	0.9	0	0	0
GALA	0	3.9	0	0	5.1	0	0	0	0
GAPR	0	0	0	2.0	0	0	0	0	0
HOCA	0	0	1.5	0	0	1.9	0	0	4.1
JUNX	0	1.3	0	0	0	0	0	0	0
KALA	30.9	9.1	5.0	37.2	14.0	15.4	53.2	20.9	16.2
LACA	0	0	0.7	0	0	0	0	0	0
LOIN	0	1.3	0	0	0	0	0	0	0
LYAN	0	0	0	9.1	0	0	0	0	0
LYOB	0	0	0	2.0	3.4	0	0	0	1.4
LYLU	0	0	0	0	0	1.9	0	0	5.4
LYQU	0	8.3	8.8	0	7.7	9.6	0	5.3	2.7
MACA	21.2	1.3	5.2	14.0	5.1	9.3	17.1	5.3	16.3
MEVI	2.7	0	1.5	0	0	0	0	0	0
MELI	0	0	3.0	0	0	3.7	0	0	1.4
MIRE	8.0	3.9	3.0	19.9	19.5	11.1	14.3	16.0	8.1
MOUN	0	0	0	0	0	0.9	0	5.3	0
PHAM	0	7.8	2.2	0	0	0	0	0	0
POAX	0	10.9	10.2	0	11.1	13.6	0	2.7	5.7
POBI	0	0	1.5	0	0	0	0	0	0
POAC	2.7	0	0	0	0	0	0	0	0
POSI	0	1.3	8.8	0	1.7	3.7	0	0	1.4
RHCO	0	1.3	0.7	0	0	0	0	0	0
RUAL	0	0	27.8	0	0	8.0	0	0	1.4
RUFL	0	3.9	0.7	0	1.7	0.9	0	0	1.4
RUID	2.7	16.5	3.7	0	8.5	0.9	0	5.3	6.8
RUOC	0	0	8.1	0	0	0.9	0	0	0
RUSE	0	0	0.7	0	0	3.7	0	0	0
SOCA	0	0	0.7	0	0	0.9	0	0	0
SORU	0	1.3	2.2	0	0	0.9	0	0	0
THNO	0	0	1.5	0	0	3.7	0	0	1.4
TRBO	21.2	1.3	11.2	29.9	3.4	12.0	31.4	13.4	19.0
TRPR	0	1.3	0	0	0	0	0	0	0
UVSE	0	0	2.2	0	1.7	4.6	0	0	1.4
VAAN	8.0	0	3.0	8.0	6.0	10.3	8.6	5.3	6.8
VACO	0	6.5	0	0	11.1	0	0	2.7	0
VAVA	2.7	0	0	2.0	0	0	0	0	0
VETH	0	1.3	0	0	0	0	0	0	0
VISO	2.7	7.8	3.7	2.0	8.5	7.4	5.7	5.3	0
VILA	0	7.8	0.7	0	6.8	2.8	0	8.0	0
VIRO	0	0	2.2	0	0	0.9	0	0	1.4

Importance value is calculated as relative frequency + relative average percent cover. Abbreviations used for the species are defined in Table 2.

(MANOVA, $F = 7.06$, d.f. = 34, 9, $P = 0.0020$). North and south edges did not have significantly different species' percent covers (MANOVA, $F = 1.28$, d.f. = 34, 9, $P = 0.3633$). Ordination revealed that early successional species were associated with center plots whereas residual species were associated with edge plots.

DCA showed that after the disturbance, all three canopy opening positions contained different suites of species than before the disturbance (Fig. 2). The south plots had a composition that was most similar to pre-disturbance composition in all years. In contrast, the species composition of center plots differed the most from pre-disturbance composition in all years. The greatest difference between center and edge plots occurred 1 year after the disturbance. The species' compositions of all gap positions began to return to pre-disturbance composition 3 years after the disturbance.

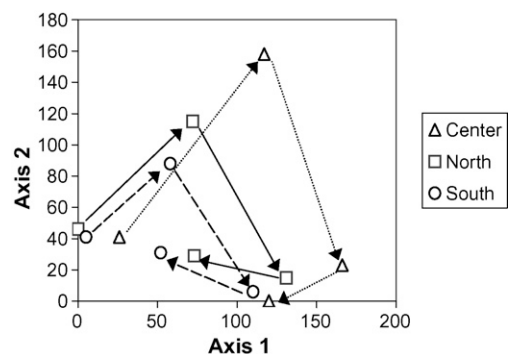


Fig. 2. Successional pathways over time of the three different gap positions (north, center, south) along the first two axes, using DCA ordination. Ordination was based on species' dominance. The first symbols for each pathway represent pre-disturbance species composition, and the arrows represent the pathway through successive years.

One year after the disturbance, center plots were very different from both edge positions (Table 4). The dominant species in all canopy opening positions were *D. punctilobula* and *C. pennsylvanica*. However, in center plots, the immigrant species *R. idaeus*, *E. hieracifolia*, and Poaceae species had high dominance values, whereas *K. latifolia* and *M. repens* had high importance values in the edge plots. Very few immigrant species had high importance values or were observed frequently in north and south plots.

Several species that were observed frequently before the disturbance decreased in frequency after the disturbance. *M. canadense* and *T. borealis* showed the largest decreases in frequency, especially in the center plots where they were observed in half of the plots before the disturbance, but only in 6.3% of the plots afterwards.

Over the next 2 years, *C. pennsylvanica* and *D. punctilobula* maintained dominance in all canopy opening positions. By 2003, immigrant species such as *R. allegheniensis* and Poaceae species continued to maintain a high presence in center plots, but residual species such as *T. borealis* had surpassed its pre-disturbance frequency and percent cover in these plots. North and south plots continued to be dominated by residual species such as *K. latifolia*, *M. canadense*, *M. repens*, and *T. borealis*.

3.4. Canopy opening position: life-history characteristics

There were significant differences between percent cover of annuals/biennials between canopy opening positions (MANOVA, $F = 4.06$, d.f. = 14, 72, $P < 0.0001$). Center plots were significantly different than north plots (MANOVA, $F = 4.51$, d.f. = 7, 36, $P = 0.0011$) and south plots ($F = 4.88$, d.f. = 7, 36, $P = 0.0006$). North and south plots were also significantly different (MANOVA, $F = 3.00$, d.f. = 7, 36, $P = 0.0138$). After the first year of disturbance, there were more annuals/biennials in the center plots than in either of the edge plots, but by 2003, the number of annuals/biennials was more similar between canopy opening positions. Generally, annuals/biennials had the highest frequencies and importance values in center and/or north plots, depending upon the species. The exception was *Aster divaricatus*, which had the highest frequencies in south plots in 2001.

Differences in evergreen species' percent covers between canopy opening positions before the disturbance were not significant, but did approach significance (MANOVA, $F = 2.10$, d.f. = 4, 82, $P = 0.0886$). After the disturbance, differences between the three plot types in terms of evergreen species' percent covers were evident (MANOVA, $F = 2.43$, d.f. = 8, 78, $P = 0.0211$). Center and north plots were significantly different (MANOVA, $F = 3.66$, d.f. = 4, 39, $P = 0.0126$). Center and south plots were not different (MANOVA, $F = 1.29$, d.f. = 4, 39, $P = 0.2908$), and although south and north plots were not different either, the P -value was approaching significance (MANOVA, $F = 2.57$, d.f. = 4, 39, $P = 0.0527$).

Five evergreen species were present before the disturbance, but only *K. latifolia* and *M. repens* survived through the disturbance, regardless of canopy opening position. *K. latifolia* had high importance values in the edge positions, and *M. repens*

had a high importance value in north plots. Colonization by several evergreen species, most notably various *Lycopodium* species in the edge plots, occurred in the years following the disturbance.

Sexually reproducing species had significantly different percent covers with regards to canopy opening position (MANOVA, $F = 2.43$, d.f. = 46, 40, $P = 0.0025$). Specifically, center plots were significantly different from north plots (MANOVA, $F = 2.68$, d.f. = 23, 20, $P = 0.0148$) and south plots (MANOVA, $F = 3.34$, d.f. = 23, 20, $P = 0.0042$). North and south plots were not significantly different (MANOVA, $F = 1.68$, d.f. = 23, 20, $P = 0.1215$).

Vegetatively reproducing species' percent covers were also significantly different between canopy opening positions (MANOVA, $F = 2.47$, d.f. = 22, 64, $P = 0.0027$). Contrasts with MANOVA showed that percent covers differed between center and north plots ($F = 2.38$, d.f. = 11, 32, $P = 0.0275$) and center and south plots ($F = 3.19$, d.f. = 11, 32, $P = 0.0050$). North and south plots were not significantly different, but the P -value was approaching significance (MANOVA, $F = 1.98$, d.f. = 11, 32, $P = 0.0658$).

The south plots were almost exclusively dominated by clonal species, whereas the center plots had a similar number of clonal and buried seed plants dominating. The north plots fell in between these two extremes with slightly more clonal plants dominating than buried seed plants. Overall, sexually reproducing species were more common and more dominant in center plots, whereas vegetatively reproducing species were more dominant in edge positions.

3.5. Disturbance intensity \times canopy opening position

Before the disturbance, percent cover of species did not differ significantly between disturbance intensity \times canopy opening position (MANOVA, $F = 1.17$, d.f. = 45, 155.2, $P = 0.2347$). However, after the disturbance, the interaction between disturbance intensity and canopy opening position resulted in significant differences in species' percent covers (MANOVA, $F = 2.41$, d.f. = 170, 49.8, $P = 0.0002$).

Table 5
MANOVA contrasts for effects of the interaction between disturbance intensity and gap position on species' percent covers

Contrast	F-Value	Num DF	Den DF	P-value
Intensity among gap positions				
Center lethal and center release	3.18	34	9	0.0352
North lethal and north release	5.21	34	9	0.0064
South lethal and south release	1.11	34	9	0.4674
Gap positions among lethal plots				
Center and north	2.78	34	9	0.0537
Center and south	3.95	34	9	0.0172
North and south	0.91	34	9	0.607
Gap positions among release plots				
Center and north	5.52	34	9	0.0052
Center and south	4.52	34	9	0.0107
North and south	1.62	34	9	0.2273

Num DF: numerator degrees of freedom; Den DF: denominator degrees of freedom.

Pairwise comparisons showed that disturbance intensity affected species' percent covers in center and north plots, but not south plots (Table 5). Among lethal plots, the center and south position had significantly different species' percent covers, but the center and north plots had only marginally significant different species' percent covers. In contrast, among release plots, the center differed more from north plots than south plots. Both lethal and release edge positions did not differ significantly.

4. Discussion

The intact forest was composed of a relatively small number of predominantly shade-tolerant shrubs and herbs characteristic of the low-light environment of a closed canopy temperate deciduous forest. The creation of the canopy opening increased resource levels, and the number of species nearly doubled in the 3 years after the disturbance. Increases in understory species richness initially after a disturbance have been documented by other studies (Halpern and Spies, 1995; Jenkins and Parker, 1999; Roberts and Zhu, 2002; Schumann et al., 2003). The change in species composition after the disturbance was due to a reduction in cover of pre-disturbance flora coupled with a large influx of immigrant species.

Although this study is pseudo-replicated and the results cannot be generalized across all eastern forests, they are congruent with successional patterns that have been observed in other studies. The differences in species composition between lethal and release plots supports observations from earlier studies in western forests in which disturbance intensity was found to affect resulting species composition (Outcalt and White, 1981; Halpern, 1988; Battles et al., 2001). Low intensity disturbances to the groundstory promote the existence and dominance of residual forest herbs and shrubs. Lethal disturbances, however, are favorable for growth and dominance of early successional immigrant species.

Minimal disturbance to the understory, such as that of release plots, allows the late successional species dominating the intact forest to survive the disturbance. This not only reduces the space available for colonization and the resources available for growth by immigrant species, but it also confers a competitive growth advantage on the residual species. Most late successional forest herbs reproduce vegetatively (Bierzychudek, 1982). Therefore, these species can take immediate advantage of the newly available resources and maintain a dominant position in minimally disturbed sites by merely expanding through vegetative reproduction. In this study, *D. punctilobula*, *C. pensylvanica*, and *K. latifolia* dominated release plots through vegetative reproduction of surviving patches. Hughes and Fahey (1991), working in a northern hardwood forest, similarly found that vegetative expansion of surviving individuals accounted for the majority of colonization of minimally disturbed sites. Other studies have also found residual species to dominate after low intensity disturbances (Halpern, 1988; Battles et al., 2001).

Lethal disturbances create an environment conducive to domination by species capable of colonizing a site quickly and growing rapidly. Although clonal species can invade a lethally

disturbed site through expansion into the gap from the edge, seed reproduction is a more effective method for colonization, especially for centers of disturbed sites. Where there is no longer a local population to expand clonally, successful colonization is dependent upon seed dispersal ability; those species in which seeds are dispersed short distances are at a disadvantage in colonizing these highly disturbed sites. In particular, ant-dispersed species such as *Trillium* cannot easily colonize highly disturbed areas. Not only do ants disperse seeds extremely short distances, but ants are also unlikely to cross unforested areas (Matlack, 1994).

In this study, early successional species such as Poaceae species, *R. ideaus*, *R. allegheniensis*, *L. quadrifolia*, *E. hieracifolia*, and *Potentilla simplex* had high importance values in lethal plots in the years after the disturbance. Mechanisms of reproduction for *L. quadrifolia* and *P. simplex* are largely unknown, but they are typical early successional species. Poaceae species and *E. hieracifolia* have wind-dispersed seeds but are also capable of germinating from buried seeds. *R. ideaus* and *R. allegheniensis* are notable for their buried seed banks. A previous study in the area found buried seed banks of old-field herbs from the time when the land was used as pasture (Ashton et al., 1998). Studies in which succession was examined after intense disturbances have found similar results (Halpern, 1988; Halpern and Spies, 1995; Fredericksen et al., 1999; Battles et al., 2001; Roberts and Zhu, 2002).

D. punctilobula and *C. pensylvanica*, residuals from the pre-disturbance flora, were also dominant in lethal plots. Colonization of lethal sites by these species may have occurred through fern spore dissemination, from buried seeds of *C. pensylvanica*, or from clonal expansion of rhizomes from the surrounding edge. *D. punctilobula*, in particular, has been shown to have rapid clonal expansion in high light conditions, explaining its dominance in lethal plots (Hill and Silander, 2001).

Overall, dominance in lethal plots was shared by many species, whereas in release plots, only a couple of species had high dominance values. Because residual species were not present in lethal plots, resources were not limiting, allowing a large number of early successional species to colonize and share dominance. In release plots, however, resources were less abundant, and colonization by early successional species less frequent. With reduced competition from early successional species in comparison to lethal plots, a few residual species were able to spread and dominate.

Although there were differences between the center and south positions in the gap, we failed to find evidence that north and center positions were similar and north and south positions were different as we hypothesized. It seems that there is a difference between the center and edge positions in general, and the orientation of the edge does not affect species' composition. Possibly, our site is not located far enough north for directional edge effects to be pronounced and noticeable. Generally, the center plots were dominated by early successional species whereas the edge plots were dominated by late successional species. Our results agree with those of McClure and Lee (1993), who studied tree regeneration in northern hardwood forest gaps. They, too, found that there was more of a center-edge effect.

By 2003, species were increasing in frequency less, but increasing in percent cover more, suggesting that new colonization was slowing, but growth of local populations, most likely from vegetative reproduction, was continuing. Many of the residual species that declined after the disturbance had already achieved or were close to achieving pre-disturbance frequencies and percent covers, even in lethal plots and center plots. Examining patterns of species' dominance after the disturbance over time suggests that much of the flora at this site that declined in abundance after the disturbance will recover. Studies on species composition of forests subjected to clearcut disturbance many years before have found that species composition in these forests resembles that of mature forests (Gilliam et al., 1995; Ruben et al., 1999; Ford et al., 2000).

However, even if the general species composition of a disturbed site is regained, not every individual species that was present before the disturbance may return to the site. Generally, loss of locally uncommon species has been reported after a disturbance (Meier et al., 1995; Roberts and Zhu, 2002), but Halpern and Spies (1995) have reported the loss of common as well as locally uncommon species. Individual species that do not return to a site should be noted and reasons for their disappearance need to be examined (Roberts and Gilliam, 1995). In this study, six species disappeared from the site and have yet to return.

Although deer are prevalent in the forest surrounding the study area, the effects of deer browsing were not included in this study. No doubt inclusion of deer browsing in the plots would have yielded different results from those we obtained as studies have shown that deer significantly affect herbaceous species density and composition (Russell et al., 2001; Horsley et al., 2003). In particular, studies have found that deer preferentially browse *Rubus* species, decreasing their cover (Tilghman, 1989; Horsley et al., 2003), while avoiding ferns and increasing their cover (de la Cretaz and Kelty, 1999; Horsley et al., 2003). Based on this, we surmise that the presence of deer would have led to a reduction of *R. ideaus* and *R. allegheniensis* in our plots. Additionally, the presence of *Rubus* inhibits fern growth (Horsley and Marquis, 1983). Thus, removal of *Rubus* through browsing coupled with the unpalatable taste of ferns would allow *D. punctilobula* to increase in cover.

Because the composition of the understory affects development of the overstory, forest managers must be cognizant of how treatments will affect the understory. After the cut, most of the experimental gap was dominated by *D. punctilobula*, regardless of disturbance intensity or position within the gap. In these areas, species that can survive seed predation and low light levels under the dense fern canopy – *Betula* species and *Pinus strobus* (de la Cretaz and Kelty, 1999) – would be most likely to grow into the overstory. The center of the gap poses additional problems for seedling growth due to the competitive mix of early successional understory species. Preliminary seedling data collected shows that although *B. lenta*, *Betula papyrifera*, and *A. rubrum* seedlings are found abundantly in the center plots, *Q. rubra* seedlings are predominantly found in edge plots. Therefore, it seems that birch, which can grow

rapidly in high light environments and successfully compete with ferns, will persist into the overstory in the center of the gap. In contrast, more shade-tolerant species such as oak will thrive on the edge of the gap where fern does not dominate.

Managers of New England mixed-oak forests concerned with natural forest plant diversity should focus on minimizing disturbance to the understory during harvesting operations and creating small openings that deter establishment of early successional species. However, although competition from early successional species is reduced with minimal disturbance, competition may still exist from dominant late successional herbs and shrubs. In this particular site, *D. punctilobula* dominated release and edge sites, and it has been shown to negatively impact seedling growth (Horsley and Marquis, 1983; de la Cretaz and Kelty, 1999, 2002; George and Bazzaz, 1999b). Thus, although minimizing disturbance and gap area reduces competition from some species, other species may still dominate in an intact understory with increased light.

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