Plant Community Succession Following Disturbances in a Pine Barren and Adjacent Hardwood Forest

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ABSTRACT

The sandstone pavement barren and adjacent cobblestone formations in Clinton County, New York were created by the sudden release of water from glacial Lake Iroquois approximately 12000 ybp. Today, the barren is a rare ecological community type in New York State, dominated by jack pine, a species that can tolerate a water- and moisture-deficient soil. The soil in the cobblestone deposits supports hardwood trees such as northern red oak, sugar maple, red maple, and American beech.

In January 1998, several days of freezing rain in the Northeast blanketed 10 million ha with 2 to 10 cm of ice. Two million ha of forests were severely affected, including the pine barren and adjacent forests in Clinton County, New York. This study investigated the effects of the ice storm and subsequent "restoration cuttings" on plant community succession in the pine barren and adjacent hardwoods. The William H. Miner Agricultural Research Institute, Chazy, New York owns the eight stands sampled in this study.

Both disturbance types had dramatic effects on plant community structure. Nearly half of the hardwood trees were severely affected by the ice storm, but most survived through epicormic branching. Understory trees and regeneration proliferated beneath the temporary canopy gaps in the main canopy. Overstory species are represented in the regeneration size classes, with shade-tolerant species being most important. In the hardwoods, neither the ice storm or restoration cuttings caused plant community succession in the strict definition; the disturbances caused shifts in importance of species present at the time the disturbances occurred rather than a replacement of one plant community by another.

In the pine barren, ice storm damage was especially intense, causing severe crown breakage in more than half of the pine trees. The majority of pine trees were killed by the ice storm and no pine seedlings were observed in the ice storm-damaged stands. Moderate amounts of jack pine regeneration (between 18000 and 24000 stems per hectare) were found in the areas treated with a restoration cutting. This amount of jack pine regeneration was considered sufficient to replace the original stand.

The future of ice storm-damaged, uncut stands in the barren is not promising. Here, the majority of pine trees are standing dead stems and the regeneration, while sparse, is primarily red maple. Without silvicultural intervention, ice storm-damaged areas of the barren will have a shift from dominance by jack pine to heath shrubs, especially black huckleberry. The restoration cutting showed that mechanical treatment, while not as effective as fire in regenerating jack pine, can bring about adequate amounts of jack pine regeneration, along with red maple, white birch and gray birch.

Keywords: plant community succession; disturbance; species diversity; ice storm; restoration cutting; hardwoods; jack pine; pitch pine; silviculture

INTRODUCTION

Ecological disturbances are "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (Pickett and White 1985). There are many different types of disturbances including meteorological (e.g., fire, wind and ice storms), hydrological (e.g., floods), geological (e.g., landslides), biological (e.g., herbivory), and anthropological (e.g., timber cutting). The sandstone pavement barren and adjacent hardwood forests in Clinton County, New York have been influenced by several of these disturbance types, with variable intensities and frequencies (Stergas and Adams 1989, Hawver 1993, Yorks and Adams 2003).

Historically, the primary disturbance type in the pine barren has been fire (Hawver 1993). The shallow soil, droughty site conditions and flammable vegetation provide a fire prone environment in the barrens. The most recent natural disturbance in the barren and adjacent forests, however, was the ice storm of January 1998 (Yorks and Adams 2003).

One of the most significant disturbances during the 20th century in the Northeast, this ice storm affected 10 million ha across southern Ontario, southern Quebec and several northeastern states. The ice storm affected 1.8 million ha in northern New York (Irland 1998), including the rare sandstone pavement barrens. The New York Natural Heritage Program ranks the sandstone pavement barrens as G2S1; these barrens are among the rarest ecological communities in New York State (Reschke 1990, Edinger et al. 2002).

The high-intensity impact of the ice storm in the Altona pine barren and adjacent hardwoods caused excessive fuel accumulation and increased the probability of uncontrollable wildfire. W.H. Miner Institute, the major property owner, decided to use timber harvest for fuel reduction, salvage and forest regeneration in selected locations on the property. These cuttings in the pine barren and adjacent hardwoods were described as "restoration cuttings." By the year 2000, the pine barren and adjacent hardwoods had stands that were disturbed by cutting and stands that were uncut, ice storm-impacted. This mosaic of forest communities provided potential for studies on the ecological effects of disturbance. Disturbances in this unique landscape became a primary focus for the Research Experiences for Undergraduates (REU) program, Center for Earth and Environmental Science at Plattsburgh State University.

The goal of this study was to evaluate the effects of two disturbance types (timber cutting and ice storm) on plant community succession in a pine barren and adjacent hardwood forest. The objectives of this study were to make comparisons between ice storm-impacted hardwood and pine barren stands (cut and uncut) based on overstory species composition, radial growth, understory, regenertion, and species diversity.

METHODS

Site Description

The study area is located in the township of Altona, Clinton County, New York. Study plots were in the pine barren (locally known as Flat Rock) and adjacent hardwood forest owned by The W.H. Miner Agricultural Research Institute. Climate data at a nearby weather station for a recent 10-year period had mean monthy air temperatures ranging from a low of -11°C in January to a high of 20°C in July. Annual frost-free periods were about 125 days. Mean annual precipitation was 82 cm. The soil in the barren is a histosol (dysic lithic borofolist, Outcrop-Ricker series). The predominant soil in the adjacent hardwoods is a spodosol (entic haplorthod, Collosse-Trout River series).

Two hardwood sites and two pine barren sites were selected for study based on the presence of permanent plots that had been installed and sampled prior to the ice storm. The hardwood sites are described as Cobblestone Hill (CH) and Atwood Road (AR). The dominant species in the hardwood stands include northern red oak (*Quercus rubra*), sugar maple (*Acer saccharum*), and American beech (*Fagus grandifolia*). The pine barren sites are designated as JP (jack pine) and JPPP (a mixture of jack pine and pitch pine (*Pinus rigida*). Each site includes an ice storm-impacted stand and a cut stand. The ice storm occurred in January 1998 and the cuttings occurred as follows: JPPP, summer 1998; JP, summer 1999; CH and AR winter 2000-01.

<u>Field Sampling</u>

Overstory trees in the hardwoods included stems ≥ 10.0 cm diameter at breast height (dbh). Because of their small size, trees in the pine barren ≥ 2.5 cm dbh were considered overstory. Overstory trees were sampled in three, 10m x 10m plots per stand. Plots were located by random compass bearings and interplot distances. Trees were recorded by species and dbh measured to the nearest 0.1 cm.

Understory trees in the hardwoods included all stems between 2.5 cm and 9.9 cm dbh. Stems were recorded as a dot tally, by species. Stems of this size were not present in the pine barren plots. Shrubs were sampled as understory vegetation in the pine barrens and recorded as percent cover by species. Understory vegetation was sampled in 5m x 5m plots located at the center of each 10m x 10m plot.

Tree regeneration included all stems ≤ 2.4 cm dbh. Stems were recorded using a dot tally, by species and type of regeneration (seedling or vegetative). Stem counts were made in 1m x 1m plots in the corners of each overstory and understory plot, for a total of 24 regeneration plots in each stand.

Percent canopy cover was measured using a concave densiometer. Densiometer readings were taken at the corners of each regeneration plot and averaged.

Tree age and radial growth measurements were obtained from red oak stumps at the Cobblestone Hill cut stand. Age and radial growth (inside bark) measurements for jack pine and pitch pine trees were obtained from previously cut (summer 2000) disks taken at ground level (Valentine 2001).

<u>Data Analysis</u>

The following variables were calculated for each stratum (overstory, understory, and regeneration) in each stand:

Density = number of stems per hectare (ha)
Dominance (trees) = basal area (m^2) = $(dbh_{cm})^2$ * 0.00007854, converted to basal area per ha
Dominance (shrubs) = % cover
Frequency = number of plots in which a species occurs
Relative Density = density of a species/ total density of all species * 100
Relative Dominance (trees) = basal area of a species/ total basal area of all species * 100
Relative Dominance (shrubs) = dominance of a species/total dominance of all species * 100
Relative Frequency = frequency of a species/ total frequency of all species *100
Importance Value (IV) (trees) = Relative Density + Relative Dominance + Relative Frequency

Importance Value (IV) (regeneration) = Relative Density + Relative Frequency

Relative Importance (RIV) = IV for a species/ total importance for all species *100
Species Diversity = Shannon-Wiener index (H^1) based on relative density

$$H^1 = -\Sigma \ln p_i * p_i$$

Where p_i = decimal fraction of relative density for each species

Pielou Evenness Index = H^1/H^1 max * 100
Where H^1 max = ln S
S = number of species (species richness)

Mean Annual Increment (MAI) per tree (cm^2 /yr) = basal area, inside bark (cm^2) / tree age

RESULTS

Table 1 compares age and tree growth between the major pine species in the barren and red oak (*Quercus rubra*), one of the predominant overstory species in the adjacent hardwoods. The average age of pitch pine (*Pinus rigida*) was 86 years; average age of jack pine (*Pinus banksiana*) was 81 years in the JPPP stand and 56 years in the JP stand. The average age of red oak trees was 91 years in the Cobblestone Hill stand.

Tree productivity as measured by radial growth rates, showed that pine trees in the pine barren increased in basal area at an average rate of 1.6 cm^2/yr, while red oak trees increased at a rate of 12.4 cm^2/yr.

Table 1. Comparison of tree ages and radial growth rates in the pine barren and Cobblestone Hill.

Stand	Species	n[1]	age[2] (yrs)	MAI[3]
JPPP	jack pine	9	81 (58-101)	1.8
JPPP	pitch pine	9	86 (46-133)	1.4
JP1	jack pine	7	56 (41-64)	1.7
CH	red oak	30	91 (62 -137)	12.4

[1] number of sample trees
[2] mean (range)
[3] mean annual increment, inside bark, (cm^2/year)

<u>Disturbance Effects in Hardwood Forests</u>

Tables 2 and 3 show that the three major species at the hardwood sites were sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), and red oak. The density of trees in the ice storm-impacted stands (500 trees per hectare (tph) at Cobblestone Hill and 767 tph at Atwood Road) was much greater than in the cut stands (67 tph at Cobblestone Hill and 233 tph at Atwood Road). Basal area in the ice storm-impacted stands (20 m^2/ha at Cobblestone Hill and 44 m^2/ha at Atwood Road) was much greater than in cut stands (2.6 m^2/ha at Cobblestone Hill and 8.8 m^2/ha at Atwood Road).

Table 2. Comparison of composition and structure in Cobblestone Hill hardwood stands.

Overstory

CUTTING (2001)

Species	Density (stems/ha)	Dominance (m^2/ha)	Freq.	RIV
Red maple	33	1.0	1	50.0
Red oak	33	1.6	1	50.0
Total	67	2.6	2	100.0

ICE STORM (1998)

Species	Density (stems/ha)	Dominance (m^2/ha)	Freq.	RIV
Sugar maple	467	16.7	3	72.5
Basswood	33	3.3	1	27.5
Total	500	20.0	4	100.0

Understory

CUTTING (2001)

Species	Density (stems/ha)	Frequency	RIV
Basswood	133	1	100.0
Total	133	1	100.0

ICE STORM (1998)

Species	Density (stems/ha)	Frequency	RIV
Basswood	400	3	41.7
Beech	533	4	34.7
Hophornbeam	267	2	23.6
Total	1200	9	100.0

Regeneration

CUTTING (2001)

Species	Density (stems/ha)	Frequency	RIV
Sugar maple	37500	18	35.1
Basswood	22500	8	18.5
Hophornbeam	8750	6	9.8
Red oak	5000	8	9.7
Beech	10000	4	8.6
Striped maple	8750	4	8.0
White ash	1667	3	3.5
Bigtooth aspen	3333	2	3.5
Black cherry	833	2	2.2
Red maple	417	1	1.1
Total	98750	56	100.0

ICE STORM (1998)

Species	Density (stems/ha)	Frequency	RIV
Sugar maple	40833	20	56.7
Hophornbeam	5833	8	13.7
Beech	5833	6	11.5
Basswood	2500	6	8.7
Red oak	1250	2	3.3
White ash	1250	2	3.3
Red maple	833	2	2.9
Total	58333	46	100.0

Understory trees were much more numerous in the ice storm-impacted stands (1200 tph) than in the cut stands (no understory at Atwood Road and 133 tph at Cobblestone Hill). The major understory species in the ice storm-impacted stands were American beech (*Fagus grandifolia*), hophornbeam (*Ostrya virginiana*), and American basswood (*Tilia americana*); (Tables 2 and 3).

Table 3. Comparison of composition and structure in Atwood Road hardwood stands.

Overstory

CUTTING (2001)

Species	Density (stems/ha)	Dominance (m^2/ha)	Freq.	RIV
Sugar maple	133	1.9	1	57.2
Red oak	67	4.1	2	28.5
White pine	33	2.8	1	14.3
Total	233	8.8	4	100.0

ICE STORM (1998)

Species	Density (stems/ha)	Dominance (m^2/ha)	Freq.	RIV
Red oak	533	41.5	2	59.8
Sugar maple	200	2.5	3	29.7
Red maple	33	0.2	1	10.5
Total	767	44.2	6	100.0

Understory

CUTTING (2001)

Species	Density (stems/ha)	Frequency	RIV
No Understory			

ICE STORM (1998)

Species	Density (stems/ha)	Frequency	RIV
Hophornbeam	933	1	55.6
Beech	267	2	44.4
Total	1200	3	100.0

Regeneration

CUTTING (2001)

Species	Density (stems/ha)	Frequency	RIV
Sugar maple	81667	20	59.8
Black cherry	10000	5	10.2
Red maple	7917	5	9.3
Hophornbeam	2917	4	5.9
Red oak	1667	4	5.3
White ash	2500	3	4.5
White pine	833	2	2.7
American elm	2500	1	2.3
Total	110001	44	100.0

ICE STORM (1998)

Species	Density (stems/ha)	Frequency	RIV
Sugar maple	20417	16	33.0
Red maple	17500	12	26.7
White pine	5417	10	14.0
Hophornbeam	5417	9	13.1
Red oak	2917	5	7.2
Black cherry	2500	1	3.2
Basswood	833	1	1.7
White ash	417	1	1.3
Total	55417	55	100.0

Tree regeneration in cut hardwood stands was 99000 stems/ha at Cobblestone Hill and 110000 stems/ha at Atwood Road (Tables 2 and 3). Tree regeneration in ice storm-impacted hardwood stands was 55000 stems/ha at Atwood Road and 58000 stems/ha at Cobblestone Hill (Tables 2 and 3). Five of the fourteen hardwood tree species observed in the regeneration size class were found in all stands; these species were sugar maple, red maple, hophornbeam, red oak and white ash (*Fraxinus americana*); (Tables 2 and 3). Sugar maple was the most important regeneration species at each site (Tables 2 and 3).

Table 4. Percent cover of overstory canopy at each study site.

Site Designation	Cover (%)
Atwood Road (Cutting)	58.1
Atwood Road (Ice Storm)	94.6
Cobblestone Hill (Cutting)	25.6
Cobblestone Hill (Ice Storm)	97.9
Jack Pine (Cutting)	0.2
Jack Pine (Ice Storm)	51.9
Jack Pine-Pitch Pine (Cutting)	5.8
Jack Pine-Pitch Pine (Ice Storm)	28.0

Table 4 shows that canopy cover (shading near ground level) was least in the cut sites (58% cover at Atwood Road and 26% cover at Cobblestone Hill) versus canopy cover near ground level in the ice storm-impacted sites (95% cover at Atwood Road and 98% cover at Cobblestone Hill).

Table 5. Shannon-Wiener diversity index (H') for tree species regeneration in the pine barren and hardwood forest.

Location	Cover Type	Disturbance Type	Species Richness	H'	Evenness (%)
CH	Hardwood	Ice Storm	7	1.137	58.5
CH	Hardwood	Cutting	10	1.763	77.0
AR	Hardwood	Ice Storm	8	1.581	76.0
AR	Hardwood	Cutting	8	0.997	48.0
Barren	Jack Pine	Ice Storm	2	0.693	100.0
Barren	Jack Pine	Cutting	5	1.052	65.4
Barren	Jack-Pitch Pine	Ice Storm	1	0.000	0.0
Barren	Jack-Pitch Pine	Cutting	5	0.962	59.8

Species diversity index values in the hardwood stands ranged between 0.9 and 1.7 (Table 5). Table 6 shows that three tree species were found at each of the hardwood stands (sugar maple, red maple, and red oak). Regeneration of hardwood trees was primarily by seedlings except at Cobblestone Hill where the cut stand had more sprouts than seedlings. At both sites, cut stands had more regeneration than ice storm impacted stands (approximately 100000 stems/ha versus approximately 55000-62000 stems/ha, respectively).

Table 6. Stem density of tree regeneration by sprouting and seed origin.

Site	Disturbance Type	Species	Density (stems/ha) Sprouts	Seedlings
Atwood Road	Ice Storm	Sugar maple	4167	16250
		White pine	0	5417
		White ash	0	417
		Hophornbeam	2917	2500
		Red oak	417	2500
		Basswood	0	833
		Red maple	4167	13333
		Black cherry	0	2500
		Total	11668	43750
Atwood Road	Cutting	Sugar maple	28333	53333
		Red oak	0	1667
		White ash	1250	1250
		Fire cherry	1667	8333
		Red maple	4167	3750
		Hophornbeam	2083	833
		White pine	0	833
		American elm	2083	417
		Total	39583	70416
Cobblestone Hill	Ice Storm	Sugar maple	0	40833
		Red maple	0	833
		Beech	833	5833
		Hophornbeam	2083	5833
		Basswood	417	2500
		Red oak	0	1250
		White ash	0	1250
		Total	3333	58332
Cobblestone Hill	Cutting	Sugar maple	13333	24000
		Basswood	20833	1700
		Red oak	2083	2917
		White ash	0	1667
		Bigtooth aspen	2917	417
		Striped maple	8333	417
		Red maple	0	417
		Hophornbeam	7917	833
		Black cherry	833	0
		Beech	10000	0
		Total	66249	32368

Disturbance Effects in Pine Barrens

Tables 7 and 8 show that the major species in the pine barren stands were jack pine and red maple. The density of trees in the ice storm-impacted stands (733 tph in both the jack pine and jack pine-pitch pine stands) was greater than the cut stands (67 tph in the jack pine-pitch pine stand and no overstory in the jack pine stand). Basal areas in the ice storm-impacted stands (9.5 m^2/ha at JP and 9.1 m^2/ha at JPPP) were much greater than cut stands (no basal area at JP and 1.7 m^2/ha at JPPP).

Table 7. Comparison of composition and structure in JP pine barren stands.

Overstory

CUTTING (1999)

Species	Density (stems/ha)	Dominance (m^2/ha)	Freq.
No Overstory			

ICE STORM (1998)

Species	Density (stems/ha)	Dominance (m^2/ha)	Freq.	RIV
Jack pine	733	9.5	3	100.0
Total	733	9.5	3	100.0

Understory

CUTTING (1999)

Species	Percent Cover	Frequency	RIV
Huckleberry	57	3	45.2
Litter	23	3	28.2
Bracken fern	13	2	17.6
Wild raisin	7	1	9.1
Total	100	9	100.0

ICE STORM (1998)

Species	Percent Cover	Frequency	RIV
Litter	60	3	48.8
Huckleberry	30	3	33.8
Blueberry	10	2	17.5
Total	100	8	100.0

Regeneration

CUTTING (1999)

Species	Density (stems/ha)	Frequency	RIV
Jack pine	9583	11	50.4
Red maple	12083	2	30.6
White birch	1250	2	8.1
Gray birch	833	2	7.3
Trembling aspen	417	1	3.6
Total	24166	18	100.0

ICE STORM (1998)

Species	Density (stems/ha)	Frequency	RIV
Red oak	417	1	50.0
Red maple	417	1	50.0
Total	833	2	100.0

Black huckleberry (*Gaylussacia baccata*) was the most abundant understory shrub in each pine barren stand, with percent cover ranging between 30% and 58% (Tables 7 and 8).

Tree regeneration in cut pine barren stands was approximately 18000 stems/ha in the jack pine-pitch pine stand and approximately 24000 stems/ha in the jack pine stand (Tables 7 and 8). Tree regeneration in ice storm-impacted pine barren stands was approximately 800 stems/ha in the jack pine stand and approximately12000 stems/ha in the jack pine-pitch pine stand (Tables 7 and 8). There were more species present in cut pine barren stands. Red maple was the most important regeneration species in the ice storm-impacted stands and jack pine was the most important regeneration species in the cut stands (Tables 7 and 8).

Table 8. Comparison of composition and structure in JPPP pine barren stands.

Overstory

Cutting (1998)

Species	Density (stems/ha)	Dominance (m^2/ha)	Freq.	RIV
Jack pine	67	1.7	2	100.0
Total	67	1.7	2	100.0

Ice Storm (1998)

Species	Density (stems/ha)	Dominance (m^2/ha)	Freq.	RIV
Pitch pine	500	8.5	3	55.5
Red maple	200	0.37	3	35.1
Jack pine	33	0.26	1	9.4
Total	733	9.1	7	100.0

Understory

Cutting (1998)

Species	Percent Cover	Frequency	RIV
Huckleberry	59	3	50.4
Litter	38	3	40.4
Mountain holly	3	1	8.6
Total	100	7	99.5

Ice Storm (1998)

Species	Percent Cover	Frequency	RIV
Huckleberry	58	3	47.8
Litter	37	3	37.3
Blueberry	5	2	15.0
Total	100	8	100.0

Regeneration

Cutting (1998)

Species	Density (stems/ha)	Frequency	RIV
Jack pine	12917	3	50.2
Paper birch	2083	3	20.7
Gray birch	833	2	12.3
Red maple	2083	1	10.7
Pitch pine	417	1	6.1
Total	18333	10	100.0

Ice Storm (1998)

Species	Density (stems/ha)	Frequency	RIV
Red maple	12083	9	100.0
Total	12083	9	100.0

Species diversity index values in the pine barren ranged between 0.0 and 1.05 (Table 5). In the pine barren, red maple regeneration was found in each stand (Table 9). Jack pine, gray birch (*Betula populifolia*), and white birch (*Betula papyrifera*) regeneration were found in the cut stands and not in the ice storm-impacted stands. Regeneration was primarily by seedlings except at JP where the cut stand had more sprouts than seedlings. At both sites, cut stands had more regeneration than ice storm-impacted stands.

Table 9. Stem density of tree regeneration by sprouting or seed origin.

Site	Disturbance Type	Species	Density (stems/ha) Sprouts	Seedlings
JP	Ice Storm	Red oak	0	417
		Red maple	0	417
		Total	0	834
JP	Cutting	Red maple	12083	0
		White birch	417	833
		Trembling aspen	0	417
		Jack pine	0	9583
		Gray birch	0	833
		Total	12500	11666
JPPP	Ice Storm	Red maple	5833	6250
		Total	5833	6250
JPPP	Cutting	Red maple	1250	833
		White birch	0	2083
		Jack pine	0	12917
		Gray birch	0	833
		Pitch pine	0	417
		Total	1250	17083

DISCUSSION

The "greater flat rock ecosystem" includes a sandstone pavement pine barren and adjacent hardwood forests on cobblestone formations. The barren is an oligotrophic site with low tree species richness (five species) and low diversity indices (H^1) for tree regeneration (0.00 to 0.96). The adjacent hardwood forests are mesotrophic sites supporting at least eight tree species, with H^1 values ranging between 0.99 and 1.76. This trend of higher species richness and higher species diversity associated with higher site quality is consistent with the individualistic hypothesis of Gleason (1926).

The ecological requirements of most tree species in northern New York cannot be satisfied on oligotrophic sites so only a few tree species are present in the barrens. The two dominant pine species in the barrens, jack pine and pitch pine, survive with extremely low radial growth rates (1.7 and 1.4 cm^2/yr, respectively). Radial growth of jack pine in Canada is commonly between 5 and 12 cm^2/yr (T. Lynham, Can. For. Serv., pers. commun.). Radial growth of red oak on the adjacent mesotrophic site is 8X greater than the radial growth of pines in the barren. Red oak trees may not survive with radial growth rates less than 2 cm^2/yr. Only one species, red maple, was present in all of the sites in this study. Red maple is exceptionally tolerant of a wide spectrum of extremes in site conditions (Burns and Honkala 1990b).

Disturbances reduce the amount of living plant biomass in ecosystems and modify the vertical structure of plant communities (Pickett and White 1985). The ice storm of 1998 and subsequent restoration cuttings in the pine barren and adjacent hardwoods had dramatic effects on community structure. In the barren, the ice storm killed over 60 percent of the trees (Adams, unpublished data). Ice storm-caused mortality in the hardwoods was lower than in the barren, between 8 and 25 percent (Adams, unpublished data), largely due to the ability of hardwood trees to recover from crown injury by producing epicormic branches. In the barren, restoration cuttings removed nearly all trees in the treated areas, similar to a clearcut in some stands and a seed tree cut in other stands. Restoration cuts in the hardwoods removed the majority of trees, similar to shelterwood or seed tree cuttings.

Another important difference between these two disturbance types is that the heavy machinery (feller-bunchers and skidders) used in the restoration cuttings reduced the density of understory trees and seedlings during the process of overstory tree removal. The machinery and tree removal also scarified the soil. The ice storm's direct impact was primarily limited to overstory trees.

Both disturbances temporarily reduced levels of plant competition and created space for plant regeneration. Direct exposure to solar radiation at ground level was increased by restoration cuttings more than by the ice storm alone. Advance regeneration, undisturbed by the ice storm, responded quickly to gaps in the overstory canopy. Changes in plant community composition are influenced by disturbance type, intensity and frequency.

Barbour et al. (1998) defined plant community succession as "a directional change in the species composition or structure of a community over time." In the hardwood stands of this study, species composition of the regeneration is similar to the composition present at the time of the disturbances. Both the ice storm and the restoration cutting appear to have caused changes in the relative importance of tree species, but did not initiate a replacement of one plant community by another. This pattern supports Egler's (1954) hypothesis of initial floristic composition for predicting species composition following a disturbance.

In the pine barren, however, there were dramatic differences in tree regeneration between the two disturbance types. In ice storm-impacted stands, pine seedlings were not present; red maple seedlings were the most abundant species in the regeneration size class. Ice storm impact may cause a replacement of jack pine by red maple. In stands that received a restoration cutting after the ice storm, jack pine regeneration was present, along with white birch, gray birch and red maple. These results were similar to those reported by Yorks and Adams (2003) and indicate that restoration cutting can be a useful tool for regenerating jack pine after ice storm damage.

Additional research will be required to determine if the relative importance of species regenerating in these stands remains similar in the future or not. Mortality rates of tree seedlings are often high. Usually, tree species show survivorship patterns intermediate between Type II and Type III (Yarranton and Yarranton 1974, Kenkel et al. 1997, Barbour et al. 1998). Therefore, in order to have important representation in the overstory of mature stands, species should have seedling densities of thousands per ha. In the hardwoods, regeneration densities were nearly 100000 stems per ha, including several species, but especially sugar maple, having seedling counts that should insure importance in the future overstory.

The absence of pine seedlings in the ice storm-impacted areas of the barren four years after the event indicates a major species loss may occur in the future. Replacement of jack pine by red maple is uncertain at this time. In the jack pine stand, the density of red maple seedlings (and red oak) was only about 400 stems per ha. This low seedling density may be insufficient to maintain red maple as a dominant overstory species in the future. Ice storm-impacted areas in the barren similar to the jack pine stand will likely become a heath barren, dominated by huckleberry and blueberry. Areas in the barren similar to ice storm-impacted jack pine-pitch pine stand may have sufficient red maple regeneration to produce a red maple overstory in the future.

The abundance of jack pine seedlings in the restoration cuts should be sufficient to maintain jack pine as the major overstory species in these areas of the barren in the future. At this time, jack pine had 50 percent of the importance in the regeneration size class. At both cut stands in this study, jack pine had nearly 10000 stems per ha, the minimum to successfully regenerate a jack pine stand (T. Lynham, Can. For. Serv., pers. commun.). Regeneration densities for red maple and white birch may also be sufficient for these species to be important overstory species in the future. If so, this would be an example of disturbance – accelerated succession (Abrams and Scott 1989).

Most hardwood species were represented in the regeneration as both seedlings and sprouts (Table 10). Regeneration of both hardwood species and pines in the barrens was primarily by seed (Table 10). American beech was the only hardwood species with sprouts, but no seedlings. The majority of species regenerating in the hardwoods are shade tolerant and most species regenerating in the barrens are shade intolerant (Table 10). These vital attributes of plant species are important to predicting plant community succession (Connell and Slatyer 1977, Cattelino et al. 1979).

The density and species composition of tree regeneration are important components of ecosystem health and integrity. Aldo Leopold (1949) was the first to use these terms in an ecological context. A precise definition of ecosystem health and integrity may not be possible, but both concepts emphasize that ecosystem stability relies on a diversity of both species and vital attributes in order to have self-recovery following disturbance (Karr and Dudley 1981, Karr 1991, Noss 1995). In this study, hardwood stands showed stability through a diversity of species and mechanisms for tree recovery and regeneration following both disturbance types. Ecosystem stability in the pine barren, however, is low in the context of ice storm disturbance. Here, the majority of trees are standing dead stems and the regeneration is sparse and consists primarily of red maple. Recovery and restoration in the pine barren following an ice storm was possible only by intervention with silvicultural treatments.

Jack pine and pitch pine are well-adapted to periodic disturbance by fire, and these ecosystems can be sustained in a variety of fire regimes (Burns and Honkala 1990a). However, each disturbance type has different ecological impacts, and these pines are not well-adapted for recovery following a high-intensity ice storm. The restoration cuttings used in this barren adequately simulated fire effects and initiated ecosystem recovery.

Table 10. Vital attributes for species comprising at least 80% of the regeneration RIV.

Species	RIV (%)	Attribute[1]
	Cobblestone Hill (Cutting)	
Sugar maple	35.1	BT
Basswood	18.5	BT
Hophornbeam	9.8	BT
Red oak	9.7	BT
Beech	8.6	VT
	Cobblestone Hill (Ice Storm)	
Sugar maple	56.7	ST
Hophornbeam	13.7	BT
Beech	11.5	BT
	Atwood Road (Cutting)	
Sugar maple	59.8	BT
Fire cherry	10.2	BI
Red maple	9.3	BT
	Atwood Road (Ice Storm)	
Sugar maple	33.0	BT
Red maple	26.7	BT
White pine	14.0	ST
Hophornbeam	13.1	BT
	Jack Pine-Pitch Pine (Cutting)	
Jack pine	52.8	SI
White birch	21.1	SI
Gray birch	12.4	SI
	Jack Pine-Pitch Pine (Ice Storm)	
Red maple	100	BT
	Jack Pine (Cutting)	
Jack pine	50.4	SI
Red maple	30.6	BT
	Jack Pine (Ice Storm)	
Red oak	50.0	ST
Red maple	50.0	ST

[1]Attribute:
V=Vegetative
S=Seedling
B=Both vegetative and seedling
I=Shade intolerant
T=Shade tolerant

CONCLUSIONS

The rare sandstone pavement barren is an oligotrophic site with low productivity, low species richness and low species diversity, while the adjacent hardwood sites on cobblestone formations are mesotrophic with moderate productivity, species richness and species diversity.

In the hardwood stands, the ice storm and restoration cuttings caused shifts in the importance of tree species but did not initiate major changes in species composition. Sugar maple will likely replace red oak as the dominant species in these stands.

The ice storm had dramatic long-term effects on the structure and composition of the jack pine barren. Most pine trees were killed by the ice storm and remain as standing, broken stems. Jack pine regeneration is absent in ice storm-impacted areas. These stands will likely become heath barrens with a sparse density of red maple.

Jack pine regeneration in the restoration cuttings is adequate to maintain jack pine as the dominant species at these sites, along with lesser amounts of white birch, gray birch and red maple.

Silvicultural intervention was necessary to maintain the ecological health and integrity of the ice storm-impacted pine barren.

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