

Harvesting impacts on soil and understory vegetation: the influence of season of harvest and within-site disturbance patterns on clear-cut aspen stands in Minnesota

Alaina L. Berger, Klaus J. Puettmann, and George E. Host

Abstract: We investigated impacts of harvesting on soil disturbance and vegetation in the aspen cover type of northern Minnesota, United States. The soil disturbance (resistance to penetration) and understory vegetation were characterized for 19 sites on five 60-m² plots placed along a disturbance gradient: landings (high harvesting traffic), skid trails (intermediate harvesting traffic), and areas off skid trails (low to no harvesting traffic). Penetration levels were quite variable, but they still indicated that within-site responses to disturbance patterns created by clear-cut harvesting were not uniform. In general, soil disturbance and understory species composition within landings were similar to those with skid trails. The soil disturbance and vegetation composition of these two levels differed from those of the low-disturbance plots (off skid trails), indicating that removing trees alone did not affect vegetation composition as much as creating an established skid trail, regardless of harvest timing. However, sites with more variable species composition (winter-harvested sites) and lower disturbance levels were less altered than sites with likely lower initial diversity (summer-harvested sites). The results suggest that it is important for recovery of understory plant communities to not only limit the amount and level of disturbances but also consider the spatial layout of harvesting, thus maintaining a spatially connected network of remnant forest patches large enough to contain interior forest species.

Résumé : Les auteurs étudié l'impact des activités de récolte sur la perturbation du sol et la végétation dans les forêts de peuplier faux-tremble du nord du Minnesota aux États-Unis. La perturbation du sol (résistance à la pénétration) et la végétation de sous-bois ont été caractérisées pour 19 sites dans cinq places-échantillons de 60 m² établies de long d'un gradient de perturbation : jetées (trafic intense), chemins de débardage (trafic moyen) et zones situées à l'écart des chemins de débardage (trafic faible à nul). Le degré de pénétration était très variable mais indiquait quand même que la réaction aux patrons de perturbation créés par la coupe à blanc dans un site n'est pas uniforme. En général, la perturbation du sol et la composition en espèces de sous-bois étaient semblables dans les jetées et les chemins de débardage. Dans les parcelles peu perturbées, à l'extérieur des chemins de débardage, la perturbation du sol et la composition en espèces étaient différentes, indiquant que le simple fait d'enlever les arbres n'avaient pas autant d'impact sur la composition de la végétation que l'établissement d'un chemin de débardage, peu importe le moment de la récolte. Cependant, les sites dont la composition en espèces étaient plus variables (sites récoltés en hiver) et le degré de perturbation moindre ont été moins modifiés que les sites avec une diversité initiale probablement plus faible (sites récoltés en été). Les résultats indiquent qu'il est important pour la récupération des communautés végétales de sous-bois de limiter non seulement la quantité et le degré de perturbation mais également de considérer la répartition spatiale des coupes pour maintenir des îlots de forêt résiduelle spatialement reliés d'une dimension suffisante pour contenir les espèces de l'intérieur de la forêt.

[Traduit par la Rédaction]

Introduction

A successful shift in management paradigm toward ecosystem management requires a thorough understanding of how forest ecosystems respond to disturbances. Disturbances, such as harvesting, are a primary factor influencing diversity and floristic composition in forested systems and have been

under great scrutiny in the last decade (Roberts and Gilliam 1995; Grace 1999). Trembling aspen (*Populus tremuloides* Michx.) is a widely distributed, shade-intolerant species that naturally regenerates through suckering after large-scale disturbances, such as fire, which remove most or all of the overstory (Perala 1990). Aspen stands typically are harvested by clear-cutting (Puettmann and Ek 1999). This method pro-

Received 27 September 2003. Accepted 21 May 2004. Published on the NRC Research Press Web site at <http://cjfr.nrc.ca> on 6 November 2004.

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vides adequate regeneration conditions for aspen (Schier et al. 1985; Perala 1990) but may not always allow persistence of associated understory species (Collins et al. 1985; Grace 1999). One of the primary types of soil disturbance created by harvesting operations is compaction through machinery traffic (Bates et al. 1993). Soil compaction has been shown to limit root growth of a variety of tree species (Ruark et al. 1982), reduce the quantity and growth of trembling aspen suckers (e.g., Shepperd 1993), and influence associated vegetation (Alban et al. 1994). Winter harvesting in northern Minnesota generally has less impact on soil properties than summer harvesting, likely because of the deep snow pack and frozen soil (Bates et al. 1993; Smidt 1996). Our study retrospectively explored the effects of disturbances, specifically harvesting, on understory vegetation. The gradient of disturbance intensities was represented by amount of harvesting traffic. In addition, we characterized the disturbance gradient by considering timing of harvest. Our objective was to test the following hypotheses: (1) soil disturbance levels differ between areas with different amounts of harvesting traffic and vary with timing of the disturbance, that is, summer or winter harvest; (2) the understory species compositions differ between areas with different disturbance levels and is influenced by the timing of disturbances.

Materials and methods

Study sites

We surveyed landowners to find recently harvested areas with trembling aspen as the dominant cover type, and we measured current conditions on those sites. Major species on the selected study sites included quaking aspen (*P. tremuloides* Michx.), bigtooth aspen (*Populus grandidentata* Michx.), and balsam poplar (*Populus balsamifera* L.). Associated species on our sites included balsam fir (*Abies balsamea* (L.) Mill.), paper birch (*Betula papyrifera* Marsh.), sugar and red maple (*Acer saccharum* Marsh., *Acer rubrum* L.), northern red oak (*Quercus rubra* L.), and American basswood (*Tilia americana* L.). Typical understory plant species found on these sites included bracken fern (*Pteridium aquilinum* (L.) Kuhn), bunchberry (*Cornus canadensis* L.), bush honeysuckle (*Diervilla lonicera* Mill.), Canada mayflower (*Maianthemum canadense* Desf.), common strawberry (*Fragaria virginiana* Duchesne), large-leaved aster (*Aster macrophyllus* L.), pale vetchling (*Lathyrus ochroleucus* Hook.), and spreading dogbane (*Apocynum androsaemifolium* L.). The study region falls within the Northern Minnesota Drift and Lake Plains section and the Western Superior Uplands section of the Minnesota Ecological Classification System (Minnesota Department of Natural Resources 2003) and has a temperate climate, with mean monthly temperatures ranging from $-18\text{ }^{\circ}\text{C}$ to $17\text{ }^{\circ}\text{C}$ and a mean annual temperature of $1.6\text{ }^{\circ}\text{C}$. Average seasonal precipitation ranges from 144 mm in winter (mostly as snow) to 122 mm in summer. Soils are derived from till plains, outwash, and moraines laid down as a result of glaciation (Anderson et al. 1996).

Measurements were in June–August of 1997 and 1998 on 19 sites that had been clear-cut between 1988 and 1994, on average 6 years before they were sampled. Average residual basal area after harvests ranged from $\leq 1\text{ m}^2/\text{ha}$ to $9 \pm 6.5\text{ m}^2/\text{ha}$. Detailed information about site conditions is presented in

Table 1. We chose sites with fairly homogeneous within-site characteristics, where mostly quaking aspen were removed through logging and no posttreatment site preparation or plantings were implemented. Areas showing other types of human or natural disturbances, such as weed control, windthrow, off-road traffic, or insect outbreaks, were avoided. Study sites ranged from 3 to 14 ha (mean, 9 ha) and were generally well suited for aspen (average aspen 50-year site index of 24 m). We split the sites into groups on the basis of season of harvest (summer or winter). Although it is likely that soils were actually frozen at the time of winter harvesting, it was not possible to confirm this.

Sample design

The plot layout was designed to cover the gradient of disturbance conditions created through harvesting traffic within each site. Harvesting patterns (network of skid trails and landings) were identified and delineated (Fig. 1). Landings receive the highest amount of traffic and thus experience the maximum harvesting soil disturbance on a site. Skid trails receive less traffic and thus less harvesting disturbance. Areas off skid trails receive little to no harvesting traffic. On each site, we placed a total of five vegetation plots ($3\text{ m} \times 20\text{ m}$) randomly within the delineated disturbance levels. Plots were placed a minimum of 25 m apart to ensure independence of the sampling points. Two plots were placed randomly in areas representing skid trails; two, in areas outside skid trails. Because there was typically only one landing on each site and we could not fit in multiple vegetation plots spaced 25 m apart, we placed only one vegetation plot randomly in landings. The plot direction was aligned with skid trails (Fig. 1). On each vegetation plot, the relevé method (Mueller-Dombois and Ellenberg 1974) was used to inventory all vascular plant species in the height stratum of 0–2.0 m. Occurrences of vascular plant species were recorded, and each species was placed in a cover class: (1) single occurrence, (2) $<5\%$ (occasional), (3) $<5\%$ (plentiful), (4) 5%–25%, (5) 26%–50%, (6) 51%–75%, and (7) 76%–100% (Greig-Smith 1964; Gauch 1984). Median percentage values were used to represent each cover class in the analysis. Nomenclature for all vascular plants followed Gleason and Cronquist (1991).

Measurements of tree regeneration were taken on one 0.001-ha regeneration plot ($2\text{ m} \times 5\text{ m}$) in the center of each vegetation plot. Residual trees were defined as trees left standing during harvest that had a minimum diameter at breast height of 18 cm. Basal area for residual trees was measured from the center of regeneration plots with a 1-m factor prism.

Because harvesting impacts, such as removal of vegetation or humus layers by the logging operation, could not be quantified 6 years after the harvest, soil disturbance was used as an indicator of harvesting traffic. Soil disturbance was characterized by measuring the resistance to penetration (kilopascals) of the mineral soil matrix with an Eijkelkamp soil cone penetrometer (Bennie and Burger 1988; American Society of Agricultural Engineers 1990). After clearing slash and the main duff layer, we pushed down on the penetrometer at a uniform rate of approximately 30 mm/s (or slower); readings were taken when the cone reached 15 cm. At a minimum, we took 10 measurements on each plot to characterize soil disturbance, ignoring readings when the penetrometer

Table 1. Site descriptions of study sites by season of harvest.

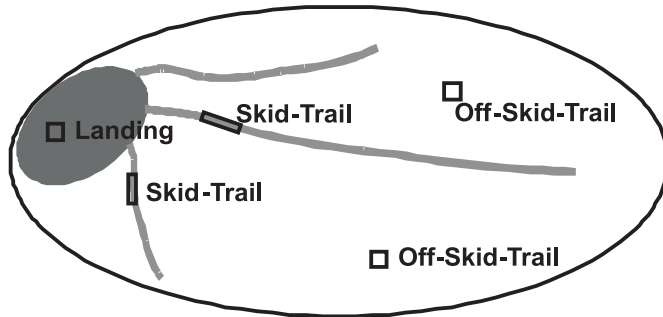
Season	Age ^a	SI (m)	Compaction (kPa)			Aspen regeneration (trees/ha)			Residual basal area (m ² /ha)		
			L	S	O	L	S	O	L	S	O
Summer (n = 45)	7	24	5599	7398 (1131)	5524 (3499)	0	2500 (3 536)	42 500 (14 849)	0	0	0.5 (0.7)
	7	23	4399	4249 (1901)	1400 (71)	0	500 (707)	11 000 (4 243)	0	1.5 (2.1)	0
	6	24	1200	1475 (177)	1200 (0)	0	500 (707)	5 500 (2 121)	4	7.5 (0.7)	12.5 (10.6)
	6	24	1550	1975 (601)	1125 (106)	0	17 000 (24 042)	37 500 (50 205)	8	0	0
	5	22	4199	4999 (0)	3799 (707)	0	5 000 (7 071)	22 500 (17 678)	0	7.5 (2.1)	13 (5.7)
	5	26	6098	5899 (1979)	4150 (2333)	0	17 500 (24 749)	29 500 (12 021)	0	0	0
	6	24	2499	2000 (141)	1350 (495)	0	0	2 500 (3 536)	4	2.5 (0.7)	3 (2.8)
	4	20	6398	3099 (706)	3299 (1273)	0	5 000 (0)	54 500 (2 121)	0	1 (1.4)	0
	5	21	7648	7898 (141)	3999 (141)	21 000	500 (707)	38 000 (24 042)	2	0.5 (0.7)	3 (2.8)
	6	23	7198	3249 (2474)	6398 (566)	0	5 000 (7 071)	35 500 (7 779)	0	0.5 (0.7)	0
Winter (n = 49)	5	23	1600	1650 (212)	2699 (707)	7 000	17 000 (2 828)	44 000 (2 828)	2	0	0
	4	23	4599	6698 (141)	2974 (672)	10 000	10 000 (4 950)	37 500 (12 021)	0	3.5 (2.1)	0
	6	23	6198	6148 (2757)	4849 (495)	0	9 000 (0)	19 500 (12 021)	0	0	1 (1.4)
	6	25	7998	6948 (71)	4249 (495)	0	3 500 (0)	47 000 (9 900)	1	1 (0)	2 (2.8)
	11	15	5399	4699 (1 838)	3699 (283)	0	0	29 000 (11 314)	0	0	1 (1.4)
	4	23	3399	5949 (707)	2100 (—) ^b	10 000	0	41 000 (—) ^b	5	0.5 (—) ^b	1 (—) ^b
	11	23	4599	5949 (71)	4049 (2333)	0	0	20 500 (4 950)	0	0	0
	8	24	3199	6248 (212)	4399 (2823)	3 000	9 500 (3 536)	11 000 (1 414)	0	0	0
	6	24	6698	4249 (636)	6498 (1273)	10 000	500 (707)	16 500 (6 364)	0	0.5 (0.7)	2 (1.4)

Note: Disturbance categories: L, landing (n = 1); S, skid trail (n = 2); O, off skid trail (n = 2). SI, aspen 50-year site index. Values in parentheses represent ±1 SE.

^aGrowing seasons since harvest.

^bMissing one off-skid-trail plot.

Fig. 1. The network of skid trails created during the harvesting operation was used to identify a gradient of harvesting traffic across each site. Relevé plots were placed in areas identified by level of harvesting traffic. One plot was placed in or adjacent to the landing, two plots were placed within skid trails, and two plots were placed off the skid trails and landing.



had obviously hit a buried rock or log. To ensure that soil moisture conditions were relatively uniform within a site, we took all measurements on the given site on a single day. Mean and median penetrometer values for the plots were correlated by an r^2 value of 0.99. Because of the high correlation and the need to minimize effects of skewness due to outlying values (e.g., resulting from “undetected” rocks), the median soil penetrometer value was used for soil disturbance values (D. Grigal, personal communication). Soil texture samples (0- to 25-cm profile) were taken from five randomly located points within each study site. We used an adapted hydrometer method to determine the soil texture (Grigal 1973).

Data treatment

Soil texture data from the study sites indicated that all are located on similar classes of sandy loams and silt loams. As expected, absolute soil disturbance levels, expressed as resistance to penetration, were quite variable. To account for other inherent site differences, such as soil moisture and topography, we standardized the median disturbance values. We assumed that areas off skid trails, although not a true control, came closest to reflecting inherent site conditions. Thus, for all plots on a site, we divided median soil disturbance and regeneration density values by the respective values in the plot least affected by harvesting (off skid trail), essentially relativizing plot values by minimum (*sensu* McCune and Grace 2002). This method of standardization was useful in a previous study on the same study sites (Arikian 2001); in that study, plots of residuals versus site index and soil texture indicated that these “standardized” disturbance and density values adequately accounted for site differences.

Floristic diversity was characterized by species richness, S (i.e., number of species/plot), and evenness, J . To calculate J , we first calculated Shannon’s index of diversity H' , using

$$[1] \quad H' = -\sum (p_i \ln p_i)$$

where p_i is the proportion of the i th species in the plot. Second, we calculated J itself from

$$[2] \quad J = H' / \ln S$$

For the purpose of detecting relationships between community composition and harvesting impacts (i.e., within the ordination and classification analysis), we reduced the influence of rare occurrences of species within the analysis by trimming species that occurred on <3 plots across all 94 vegetation plots (Legendre and Legendre 1998).

Analysis

We used JMP 3.1 (SAS Institute Inc. 1999) to perform analysis of variance (ANOVA) and examined histograms of data within disturbance categories for evidence of outliers. If ANOVA results were significant, we used the Tukey–Kramer HSD multiple comparison of means procedure, which preserves an experiment-wise error rate of 0.05. We applied a modified least significant difference test (Welch 1951) when variances within groups were unequal. Throughout the analysis, “significant” and “highly significant” refer to $\alpha \leq 0.05$ and $\alpha \leq 0.01$, respectively.

ANOVA and Tukey–Kramer HSD procedures were used to test whether areas in landings, areas on skid trails, and areas off skid trails and landings varied in their soil disturbance values, and whether soil disturbance values differed between sites harvested in summer and those harvested in winter. To sort out potential effects of confounding factors, we used ANOVA and Tukey–Kramer HSD tests for residual overstory (basal area) and soil texture (percent sand) to compare sites disturbed in summer and those disturbed in winter. The same procedures were also used to investigate impacts of harvesting disturbances on aspen regeneration (standardized trees per hectare) and understorey S and understorey J by disturbance level and season of harvest.

We used PC-ORD 3.05 (McCune and Mefford 1997) for ordination and classification analysis. Outlier analysis within PC-ORD used a cutoff of 2 SD of the Euclidean distance and inspected graphical placement of plots along ordination axes. Detrended correspondence analysis (DCA) (Hill and Gauch 1980; Ter Braak 1995) was used to explore the relationships between plots, on the basis of understorey species composition, and the influence of disturbance level (landing, skid trail, and off skid trail) and season (summer and winter harvests) on the groups. Given the focus on detecting patterns in understorey vegetation rather than aspen regeneration, we improved resolution of the ordination axis by removing aspen species from the species by plot matrix. Interpretation of variation along DCA axes was aided by construction of a second matrix, with the following categorical variables: disturbance level (landing, skid trail, and off skid trail) and season harvest (summer and winter harvests).

A nonparametric classification procedure was used to test the significance of species composition within the disturbance level by season of harvest matrix. The procedure compares the plots within categorical groups to a random allocation of plots by using the multiresponse permutation procedure (MRPP) and is useful in conjunction with multivariate analysis, as there is no requirement for normal distributions of data (Mielke 1984; Zimmerman et al. 1985).

For categorical groups determined to be significant in uniquely identifying species assemblages, indicator species analysis was used to identify the specific species characteristic of those groups. In this method, an indicator index value (IV) is assigned to a species on the basis of a combination of

Table 2. ANOVA and Tukey–Kramer HSD means comparisons for standardized disturbance levels (A) by disturbance category and (B) by season of harvest (summer or winter, with disturbance categories combined).

(A) By disturbance category.				
Disturbance	Summer		Winter	
	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>
L	214.38±23.54a	8	156.44±19.61ab	9
S	204.5±16.65a	16	164.72±13.86a	18
O	129.06±16.65b	16	110.81±14.70b	16
	$F_{[2]} = 6.77$ $P = 0.003$		$F_{[2]} = 9.35$ $P = 0.002$	
(B) By season of harvest.				
Season	L and S plots		O plots	
	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>
Summer	207.79±14.84a	24	129.06±9.62a	16
Winter	161.9±13.99b	27	110.81±9.62a	16
	$F_{[1]} = 5.05$ $P = 0.029$		$F_{[1]} = 1.80$ $P = 0.20$	

Note: Different lower-case letters indicate significantly different ($P = 0.05$) means for disturbance categories. ANOVA, analysis of variance; L, landing; S, skid trail; O, off skid trail; SE, standard error.

the species' relative abundance and relative frequency values (McCune and Grace 2002):

$$[3] \quad IV_{kj} = 100(RA_{kj} \times RF_{kj})$$

where RA is the relative abundance of a species j in group k (this measures the exclusiveness, or the concentration of abundance in a particular group); and RF is the relative frequency of species j in group k . We tested the null hypothesis (species had no indicator value), using a Monte Carlo permutation technique and 1000 permutations (Dufrene and Legendre 1997).

Results and discussion

Soil disturbance

As expected, the resistance to penetration was quite variable between and within sites (Table 1). However, despite the variability, soil disturbance levels showed significant trends. Average soil disturbance levels (standardized) in landings were essentially the same as those on skid trails for sites harvested in summer and in winter (Table 2A). On summer-harvested sites, soil disturbance levels in both landing and skid-trail plots were significantly greater than in off-skid-trail plots. On winter-harvested sites, soil disturbance levels in the landing and skid-trail plots were greater than in the off-skid-trail plots; however, these differences were significant only between the skid-trail plots (not the landing plots) and the off-skid-trail plots (Table 2A).

Because of the aforementioned results, landing and skid-trail plots were combined for testing the influence of disturbance timing on soil disturbance. Summer-harvested sites showed higher average soil disturbance levels in disturbed areas (landing and skid-trail plots combined) than

winter-harvested sites (Table 2B). This result was related to disturbance timing, rather than to inherent site differences, as evidenced by the lack of differences in disturbance levels between summer- and winter-harvested sites for the off-skid-trail conditions (Table 2B). Although the exact conditions during the harvesting operation on our sites were not documented, the seasonal differences in soil disturbance can likely be attributed to the presence of a protective snow layer and (or) frozen soil (Mace et al. 1971).

Tree regeneration, residual overstory, and soil texture

Aspen regeneration density is a response to soil disturbance and thus differs between high-impact (skid trails and landings) and low-impact areas (off skid trails) (Table 3). This may be due to a combination of decreased soil aeration and damaged roots (Shetron et al. 1988), which decreases the growth potential of roots and the ability of aspen to sucker (Stone and Elioff 1998). Also, aspen suckering is known to vary by season of harvest (Zehngraff 1946; Steneker 1974; Smidt 1996). This phenomenon has been attributed to lower aspen root carbohydrate stores in spring and early summer (Schier 1981).

Aspen regeneration density may also affect understory vegetation, and its effects cannot clearly be distinguished from the direct impact of the harvesting operation through soil disturbance. Thus, any interpretation of the vegetation patterns must include both direct (through soil disturbance) and indirect (through aspen regeneration density) impacts. Although we could not assess the importance of each of these components over the disturbance gradient, the effects of competition from aspen regeneration on understory plant composition were judged by their influence on off-skid-trail plots. Off-skid-trail plots were chosen for this assessment because they contained the highest aspen regeneration densities (Table 3) and lowest disturbance values (Table 2A). Aspen regeneration density on off-skid-trail plots was not significantly different by season of harvest ($F_{[2]} = 0.81$, $P = 0.38$). In addition, mean species richness was higher on winter-harvested off-skid-trail plots (Table 4A), indicating that competition from aspen regeneration was not responsible for lowering diversity on summer-harvested sites. At the same time, residual overstory density for summer- and winter-harvested sites did not differ between disturbance categories ($F_{[2]} = 0.17$, $P = 0.85$ for summer-harvested sites; $F_{[2]} = 0.06$, $P = 0.94$ for winter-harvested sites), whereas soil texture, expressed as percentage sand, was significantly greater for summer-harvested sites ($F_{[2]} = 17.60$, $P < 0.0001$).

Floristic composition

Disturbance categories (landing, skid trail, and off skid trail) were useful in identifying the major compositional patterns in DCA on summer- and winter-harvested sites (Figs. 2A and 2B). For summer-harvested sites, axes I and II explained 32% of the variation and represented the major compositional gradients. Axis II scores seemed most closely related to the disturbance categories, with high scores for most of the off-skid-trail vegetation plots. Landing and skid-trail vegetation plots greatly overlap in ordination space, with low DCA scores for axis II, indicating their similarity in plant composition. Scores for off-skid-trail vegetation plots slightly overlap those of the landing and skid-trail

Table 3. ANOVA and Tukey–Kramer HSD means comparisons for standardized aspen regeneration density and residual basal area in disturbance categories.

Disturbance	Summer (mean ± SE)			Winter (mean ± SE)		
	Regeneration	Residual basal area (m ² /ha)	<i>n</i>	Regeneration	Residual basal area (m ² /ha)	<i>n</i>
L	12.5±15.80a	2.25±1.36a	8	19.00±8.88a	0.67±0.45a	9
S	12.38±11.17a	1.63±0.96a	16	12.78±6.28a	0.67±0.32a	18
O	94.19±11.17b	2.38±0.96a	16	102.0±6.66b	0.81±0.34a	16
	$F_{[2]} = 16.08$ $P = 0.001$	$F_{[2]} = 0.17$ $P = 0.85$		$F_{[2]} = 53.93$ $P < 0.001$	$F_{[2]} = 0.06$ $P = 0.94$	

Note: Grouped by season of harvest. Different lower-case letters indicate significantly different ($P = 0.05$) means for disturbance categories. ANOVA, analysis of variance; L, landing; S, skid trail; O, off skid trail.

Table 4. ANOVA and Tukey–Kramer HSD means comparisons for richness and evenness (A) by disturbance category and (B) by season of harvest, with disturbance categories combined.

(A) By disturbance category.						
Season	L and S plots (mean ± SE)			O plots (mean ± SE)		
	Richness	Evenness	<i>n</i>	Richness	Evenness	<i>n</i>
Summer	38.88±1.38a	0.77±0.02a	24	30.47±1.64a	0.80±0.03a	15
Winter	43.15±1.30b	0.85±0.02b	27	37.75±1.59b	0.83±0.02a	16
	$F_{[1]} = 5.05$ $P = 0.029$	$F_{[1]} = 9.42$ $P = 0.004$		$F_{[1]} = 10.19$ $P = 0.003$	$F_{[1]} = 0.80$ $P = 0.38$	
(B) By season of harvest.						
Disturbance	Summer (mean ± SE)			Winter (mean ± SE)		
	Richness	Evenness	<i>n</i>	Richness	Evenness	<i>n</i>
L	38.63±2.17a	0.79±0.04a	8	41.67±2.38ab	0.81±0.03a	9
S	39.0±1.54a	0.77±0.03a	16	43.89±1.68a	0.86±0.02a	18
O	30.47±1.59b	0.80±0.03a	15	37.75±1.78b	0.83±0.02a	16
	$F_{[2]} = 8.66$ $P = 0.001$	$F_{[2]} = 0.27$ $P = 0.766$		$F_{[2]} = 3.17$ $P = 0.053$	$F_{[2]} = 1.39$ $P = 0.26$	

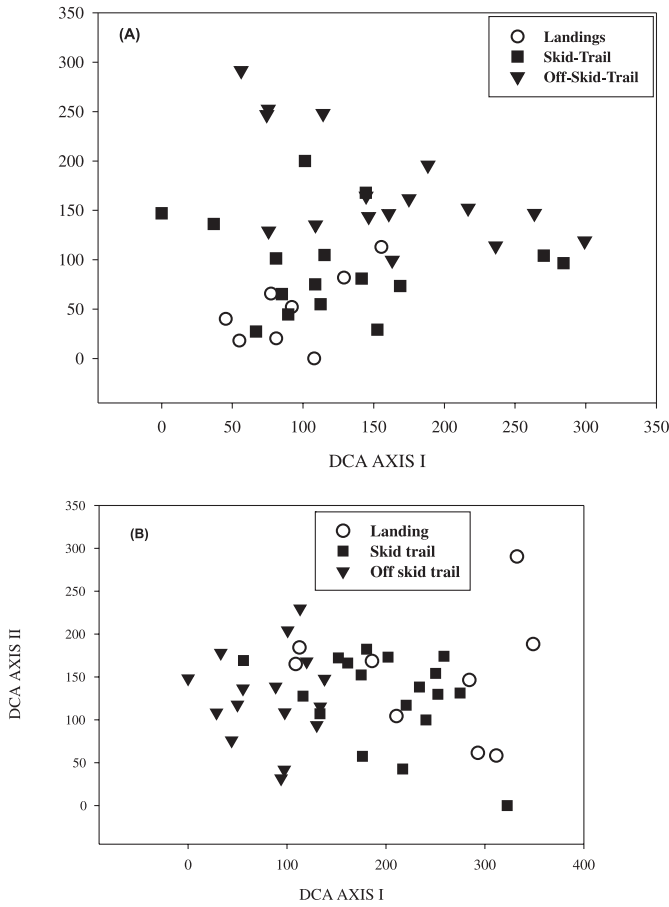
Note: Different lower-case letters indicate significantly different ($P = 0.05$) means for disturbance categories. L, landing; S, skid trail; O, off skid trail; SE, standard error.

vegetation plots, but the off-skid-trail plots still appear as a distinct group (Fig. 2A). Indirect effects (through tree regeneration) of the harvesting disturbance are reflected in the summer-harvested sites with axis II scores correlated with tree regeneration density (adjusted $R^2 = 0.345$, $P < 0.001$). MRPP analyses confirmed these findings, showing that species composition was not significantly different between landing and skid-trail vegetation plots ($T = 0.34$, $P = 0.28$). However, vegetation composition in off-skid-trail plots was distinctly different from that of the landing and skid-trail plots combined ($T = -4.31$, $P < 0.004$). Similarly, DCA of winter vegetation plots revealed that axes I and II were the major gradients, explaining 30% of the variation. Axis I scores were most closely related to the disturbance categories, with high scores for the landing and skid-trail vegetation plots. Scores for the landing and skid-trail vegetation plots overlapped, whereas off-skid-trail plot scores remained more distinct (Fig. 2B). Indirect effects of the harvesting disturbance are reflected as well within the winter-harvested sites, with a correlation between axis I scores and tree regeneration densities (adjusted $R^2 = 0.397$, $p < 0.001$). MRPP was able to distinguish landing vegetation from skid-trail vegetation, as well as distinguish each of these from the

off-skid-trail vegetation. Each disturbance category was significantly distinct in vegetative composition (landing vs. skid trail, $T = -1.91$, $P = 0.05$; skid trail vs. off skid trail, $T = -6.77$, $P < 0.001$; landing vs. off skid trail, $T = -4.29$, $P = 0.001$). This indicated that clearcuts resulted in a range of disturbance levels and thus diversity of conditions for plant establishment and growth, reflected in a diversity of understory vegetation (Harrington and Edwards 1999). At a different scale, Battles et al. (2001) found the greatest diversity of plant species under the most intensive silvicultural treatments, and the typical species composition of forest stands was conserved only in the least intensive treatment.

DCA of vegetation data from all disturbance categories combined did not show distinctly separate groups by season of harvest. Because the off-skid-trail category of vegetation plots had the lowest levels of disturbance and had a distinctly different vegetation composition, inclusion of these plots might have disguised the influence of season of harvest on species composition. To avoid this, we removed off-skid-trail vegetation plots and conducted a revised ordination. The revised ordination revealed that axes I and II explained 37% of the variation (Fig. 3A). Summer-harvested plots, although somewhat overlapping winter-harvested

Fig. 2. Detrended correspondence analysis (DCA) of floristic composition in (A) summer-harvested plots and (B) winter-harvested plots, as influenced by harvesting traffic.

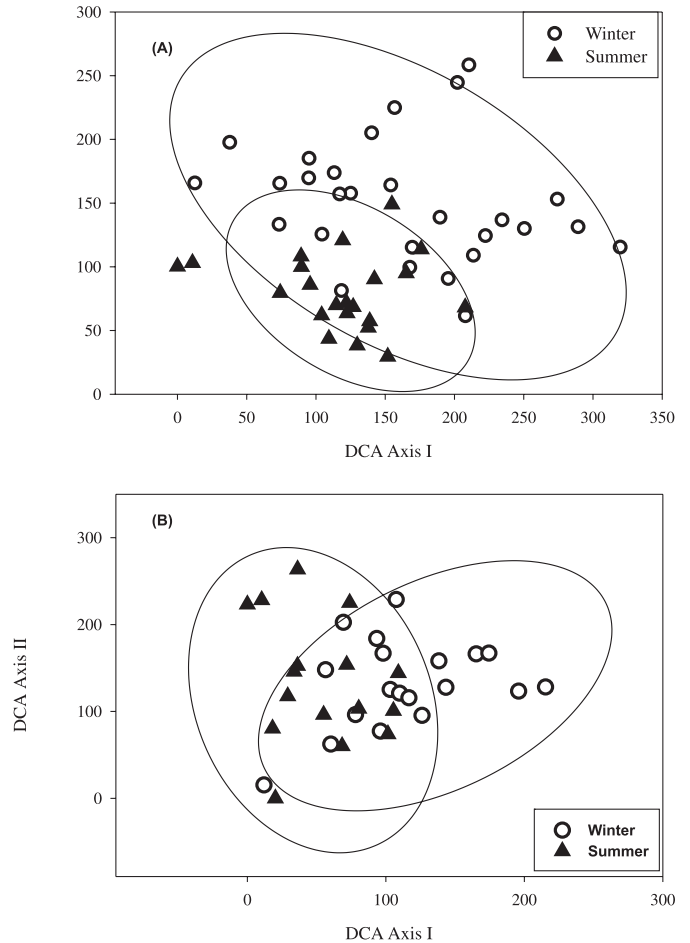


plots, were more tightly clustered into a distinct cloud ($\delta = 60.7$) than the winter-harvested plots ($\delta = 66.1$) (Fig. 3A). MRPP confirmed the distinctness of species composition by season of harvest for landing and skid-trail plots combined ($T = -4.13$, $P = 0.005$). Small and McCarthy (2002) suggested that these patterns may be due to stressful conditions created for interior forest plants on landings and skid trails via the combined alteration of competitive and microclimate conditions and soil disturbance.

To assess whether this difference might be related to inherent site differences in summer- and winter-harvested sites, rather than to harvesting disturbance, we conducted an ordination of only off-skid-trail vegetation plots. Summer- and winter-harvested off-skid-trail vegetation plots overlap along both axis I and axis II and reflect less coherent groups by season of harvest (Fig. 3B). Although plots appeared to group slightly in ordination space, MRPP did not detect a difference in species composition by season ($T = -0.59$, $P = 0.24$). In addition, differences in variability of species composition by season were less distinct ($\delta = 68.7$ and $\delta = 72.5$ for summer and winter, respectively), indicating no inherent differences in vegetation composition between summer- and winter-harvested sites.

We identified indicative species for both summer and winter sites by combining landing and skid-trail plots versus off-skid-trail plots, resulting in two main disturbance categories

Fig. 3. Detrended correspondence analysis (DCA) of floristic composition in (A) high-traffic (landing and skid trail combined) vegetation plots and (B) low-traffic areas (i.e., off skid trails). Bivariate ellipses represent 95% of data within season of harvest categories.



ries (high and low). Species found to be significant for identifying high- or low-disturbance categories overlapped by season of harvest (Table 5). Both sites harvested in winter and those harvested in summer revealed a compositional shift (dominance) of species. This confirms findings from northern British Columbia (Haeussler et al. 1999) and mixed conifer–deciduous forest in New Brunswick (Roberts and Zhu 2002), where species composition varied with intensity of disturbance in recent clearcuts. As in our study, compositional differences were related to higher abundance of nonnative species occupying the most intensely disturbed areas (Haeussler et al. 1999). On the other hand, in boreal mixedwoods the diversity of understory vegetation increased in areas with site preparation, compared with undisturbed sites, but did not vary according to intensity of disturbance (Peltzer et al. 2000). Our results indicate that diversity and composition patterns within a site existed as a matrix of patches (disturbance levels) with different diversity patterns, highlighting that harvesting is acting as a disturbance through various processes (sensu Roberts and Gilliam 2003). For example, composition of the herbaceous layer after harvest is clearly influenced by alterations in competitive pat-

Table 5. Species indicative of disturbance categories within summer-harvested and winter-harvested sites.

Disturbance level	Species	Maximum importance index	
Summer			
High	<i>Agrostis gigantea</i> Roth.	29	
	<i>Betula papyrifera</i> Marsh.	70	
	<i>Erigeron strigosus</i> Muhl.	33	
	<i>Fragaria virginiana</i> Duch.	68	
	<i>Geum aleppicum</i> Jacq.	33	
	<i>Juncus tenuis</i> Willd.	33	
	<i>Phleum pratense</i> L.	33	
	<i>Poa</i> L. spp.	33	
	<i>Rubus idaeus</i> L.	68	
	<i>Taraxacum officinale</i> Web. ex Wigg.	74	
	Low	<i>Abies balsamea</i> (L.) Mill.	44
		<i>Acer rubrum</i> L.	55
		<i>Acer saccharum</i> L.	56
		<i>Acer spicatum</i> Lam.	48
<i>Anemone quinquefolia</i> L.		41	
<i>Apocynum androsaemifolium</i> L.		40	
<i>Aralia nudicaulis</i> L.		80	
<i>Clintonia borealis</i> (Ait.) Raf.		57	
<i>Corylus cornuta</i> Marsh.		75	
<i>Impatiens capensis</i> Meerb.		19	
<i>Lonicera canadensis</i> Marsh.		45	
<i>Maianthemum canadense</i> Desf.		65	
<i>Rubus pubescens</i> Michx.		46	
<i>Streptopus roseus</i> Michx.		47	
Winter			
High	<i>Achillea millefolium</i> L.	26	
	<i>Agrostis gigantea</i> Roth.	30	
	<i>Betula papyrifera</i> Marsh.	60	
	<i>Carex</i> L. spp. (Ovales type)	43	
	<i>Fragaria virginiana</i> Duch.	77	
	<i>Juncus tenuis</i> Willd.	30	
	<i>Onoclea sensibilis</i> L.	22	
	<i>Phleum pratense</i> L.	33	
	<i>Poa</i> L. spp.	33	
	<i>Prunella vulgaris</i> L.	30	
	<i>Rubus idaeus</i> L.	73	
	<i>Salix</i> L. spp.	55	
	<i>Scirpus cyperinus</i> (L.) Kunth.	44	
	<i>Taraxacum officinale</i> Web. ex Wigg.	52	
	<i>Trifolium hybridum</i> L.	37	
	Low	<i>Anemone quinquefolia</i> L.	56
		<i>Aralia nudicaulis</i> L.	81
<i>Aster macrophyllus</i> L.		79	
<i>Botrychium virginianum</i> L. (Sw.)		21	
<i>Carex pensylvanica</i> Lam.		41	
<i>Clintonia borealis</i> (Ait.) Raf.		45	
<i>Cornus alternifolia</i> Lf.		38	
<i>Corylus cornuta</i> Marsh.		69	
<i>Lonicera canadensis</i> Marsh.		37	
<i>Maianthemum canadense</i> Desf.		50	
<i>Oryzopsis asperifolia</i> Michx.		54	
<i>Osmorhiza claytonii</i> Michx. CB. Clarke		41	
<i>Ribes cynosbati</i> L.		25	
<i>Rubus pubescens</i> Raf.		64	
<i>Tilia americana</i> L.	47		
<i>Trientalis borealis</i> Raf.	39		
<i>Ulmus americana</i> L.	22		
<i>Uvularia sessilifolia</i> L.	30		

Note: The maximum index value (%) was used to test significance for species by disturbance category ($P \leq 0.05$).

terns, mostly a reduction of competition from higher strata. This may have been an influential factor in areas outside skid trails. Processes related to substrate modification and damage to plants were likely very influential in landings and skid trails (Roberts and Gilliam 2003).

Although the overall pattern of greater dominance by ruderal species on high-disturbance plots was similar in winter- and summer-harvested sites, there was evidence that winter-harvested sites were more inherently mesic in species composition, with species suited to moist conditions present on both high- and low-disturbance plots. Mean species richness in vegetation plots was not significantly different between high-disturbance (landings) and intermediate-disturbance (skid trail) categories for either season (Table 4B). Although both landing and skid-trail disturbance plots had significantly greater mean richness than off-skid-trail plots in summer-harvested sites, in winter-harvested sites only the mean richness of skid-trail plots was significantly greater than in off-skid-trail plots (Table 4B.). Mean evenness of species for plots on summer- and winter-harvested sites was not significantly different for any category of disturbance ($F_{[2]} = 0.27$, $P = 0.766$; $F_{[2]} = 1.39$, $P = 0.26$ for summer and winter, respectively). Regarding the impact of inherent site differences in summer and winter sites (i.e., using only off-skid-trail vegetation plots), mean richness was significantly higher for winter-harvested sites ($F_{[1]} = 10.19$, $P = 0.003$), whereas mean evenness was not significantly different by season of harvest ($F_{[1]} = 0.80$, $P = 0.38$). However, mean richness and evenness on the high-disturbance (landing and skid trail) vegetation plots combined were significantly lower on summer-harvested sites (Table 4A). These findings support De Grandpré and Bergeron's (1997) conclusions that change in plant composition is less in more diverse environments, even though one must consider the fact that in our study the disturbance (measured as resistance to soil penetration) was also lower in the more diverse sites.

The length of the impact of harvesting traffic on soil and vegetation is uncertain. Evidence in an Appalachian hardwood forest indicates that spatial links between understory diversity, biotic (e.g., tree density), and abiotic factors were still detectable 20 years after harvest (Gilliam 2002). The question of recovery time is especially important in aspen stands, where a rotation can be as short as 40 years. The spatial layout of landings and skid trails may have a direct impact on the patterns of future understory vegetation recovery (Hughes and Fahey 1991), as initial and remnant understory vegetation of harvested sites has been linked to the rate of recovery (Rydgren et al. 1998), with higher proportions of ruderal species extending the recovery time, as well as altering the trajectory of the site (Halpern 1988). Patches with low disturbance, such as off-skid-trail areas, have been shown to act as species pools (Zobel 1997), which can provide a source of interior forest species to recolonize the site. Interior forest species might be available to colonize more disturbed patches, but they are often less competitive than ruderal species in harsh microclimates (Meier et al. 1995). Thus, competition between interior forest species and ruderal species could slow the rate of recovery or even alter the long-term composition of the site by encouraging more ruderal species in the soil seed bank (Yorks and Dabydeen 1999). For all these reasons, maintaining a spatially connected network of

remnant forest patches that are large enough to contain viable interior forest species seems to be desirable in harvesting operations.

Acknowledgements

Funding for this study was provided by the Minnesota Forest Resources Council, the USDA Forest Service North Central Research Station, and the University of Minnesota College of Natural Resources. This work was conducted while the two lead authors were with the Department of Forest Resources, University of Minnesota, St. Paul, Minnesota. We would like to thank J. Zasada for his help in study design, M. Arikian and D. Stangle for their help with field measurements, and a number of foresters for their assistance in study site selection.

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