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Effects of edges on plant communities in a managed landscape in northern Wisconsin

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Abstract

The effects of edges on plant communities following clearing of coniferous forests in the Great Lakes region had not been previously examined. This study quantified plant responses to six recent (8–12 years old) clearcut edges adjacent to jack pine (*Pinus banksiana*) and red pine (*Pinus resinosa*) plantations. Percent cover of each understory plant species was estimated within 10 randomly placed plots at 19 distances along a 240 m transect extending from the clearcut, across the edge, and into the forest interior. Species richness was significantly higher in the jack pine stands (n=10.2–12.2) than in the red pine stands (n=6.1–9.1, p<0.05). Among the 67 species detected, 18 and two species were unique to the jack and red pine stands, respectively. Detrended correspondence analysis (DCA) and abundance band ratios were used to divide species into functional groups according to their distributions along the transect. A depth-of-edge influence was determined for species that showed a clear preference for the clearcut, interior, or edge habitat. Compositional gradients were also reflected in a DCA of distance sampled based on species abundance. Finally, regression models were developed to predict diversity from topographic, structural, and stand composition variables. A synthesis model is presented to describe plant species distributions across forest/clearcut edges. In this model, edge species patterns can show stronger effects on one side of the forest/clearcut edge than the other side. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Chequamegon National Forest; Edge effects; Plant species; Fragmentation; Diversity; Depth-of-edge influence; Management practices

1. Introduction

In the upper Great Lakes region of the US, forest management regimes vary from partial cutting (individually selecting trees from various size classes for harvest) to clearcutting (removal of all trees in a single harvest; USDA, 1994). A significant portion of these contiguous forests has been clearcut. Given that the timber industry continues to act as a dominant source of income for this area, it is important to assess how management regimes affect these ecosystems (USDA, 1994). In particular, biodiversity of understory plant species may be a concern of land managers since these plants may indicate site quality and ecosystem health (Forman, 1995, Turner, 1996).

Previous studies have examined edge effects by placing vegetation sampling plots near the forest boundary, but located exclusively within the interior (Cadenasso et al., 1997). No known studies in the upper Great Lakes region have examined clearcut-edge-pine plantation gradients using a transect sampling design, though this approach has been implemented in the

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Pacific Northwest (Chen et al., 1993). We investigated edge effects at plantations of red pine (*Pinus resinosa*) and jack pine (*Pinus banksiana*), species of high commercial value and the focus of many management practices in the upper Great Lakes region (USDA, 1994). We explored the clearcut edge effects by following the gradient from the clearcut through the area of edge influence (AEI) to the forest interior at recent (8–12 years) jack or red pine plantation harvests in the Chequamegon National Forest in northern Wisconsin. In this study we attempted to answer three questions:

1. Is there an effect in terms of understory plant species composition and abundance when crossing from a clearcut to an edge to the forest interior in two different types of pine plantations?
2. What are the differences in the effects of edges on understory composition between the red and jack pine plantations?
3. How well can species diversity and total estimated understory cover be predicted from a combination of variables pertaining to forest structure, topography, and composition?

We hypothesized that understory species would differ in relative and total abundance between the edge, plantation, and clearcut. We expected that effects of edges on understory plant frequency, abundance, and diversity would differ between the jack and red pine plantations. Therefore, understory species can be divided into functional groups based on their changes in abundance with distance from the edge, and a depth-of-edge influence (DEI) was determined on a species by species basis. Finally, multiple regression models were implemented to assess the ability to predict diversity from topographic, structural, and stand composition variables within these specific sites. We expected that significant diversity predictors would be percent canopy cover, estimated percent coarse woody debris cover, and total estimated grass cover.

2. Materials and methods

2.1. Study area

The study area was located within the Washburn Ranger District of the Chequamegon National Forest, WI, USA (46°30′–46°45′N, 91°02′–91°22′W). Red pine and jack pine plantations established in the 1930s comprise a significant portion of the landscape (35%, Brosofske, 1999). These plantations are found on areas that had been occupied by either pine barrens or northern dry forest vegetative communities prior to European settlement in the 1800s. The disturbance regimes within the jack pine and red pine differ in intensity. The red pine plantations are subject to low-intensity regimes, such as partial cutting every 10–15 years, while high intensity disturbance events, such as shelterwood or overstory removal treatments take place every 100–150 years. The high intensity disturbance regime within the jack pine plantations consists of 40–70 year intervals between clearcuts (USDA, 1994). When these areas are clearcut, no trees are left standing, but are generally replanted.

The landscape is characterized by late Wisconsin-age glaciated landscapes and Precambrian shield bedrock. Topography is flat to rolling with elevations ranging from 232 to 459 m. Between 66–70 cm of rain and 106–150 cm of snow falls as precipitation each year, and the growing season spans from 120 to 140 days. The bedrock geology is characterized by Precambrian and Cambrian bedrock covered with 34–200 m of glacial drift. The soils are deep loamy sands with little organic matter and are classified as Psamments and Orthods (Albert, 1995).

2.2. Sampling

Three red pine plantation-clearcut and three jack pine plantation-clearcut edges (all north-facing) were selected based on initial examination of aerial photos, the year of the clearcut (i.e. edge age, 8–12 years), and their distance to other edges (such as roads) in 1998. No site closer than 100 m to any other edge was selected in order to reduce confounding relationships, such as multiple edge effects and heterogeneous vegetation communities within the forests.

All sampling was performed from late June to mid-August 1998. The edge zone was initially defined from the distances that extended from 5 m into the forest and 5 m into the clearcut. The clearcut was the area from 10 to 120 m into the clearcut, and the forest interior extended from 10 to 120 m into the plantation. Understory vegetation was sampled at the edge and at distances of 5, 10, 15, 20, 30, 45, 60, 90, and 120 m from the edge into the adjacent clearcut and forest interior. The distance of 120 m was selected as a maximum since it is at least twice the length at which edge effects in the understory of temperate forests in the eastern US have been noted (Palik and Murphy, 1990; Fraver, 1994; Matlack, 1994). A greater number of distances closer to the edge were sampled in order to capture dramatic changes near the edge and accurately determine the depth-of-edge influence. A species-area relationship was constructed using preliminary data collected in 1996 to determine that 10 plots were needed to quantify the community composition (Magurran, 1988). Hence, at each distance, 10 randomly placed 1 m×1 m plots, five on either side of the transect, were inventoried making a total of 190 plots per site. In addition to estimates of percent cover of understory vegetation by species, other variables we recorded included percentage of bare ground, duff depth (cm), slope (%), position on slope % (five categories), aspect (%), understory cover classes, percent and diameter of stump cover, percent cover of coarse woody debris, and percent canopy cover (using a spherical densiometer). Understory cover classes were visually estimated by percent total understory from 0–0.5, 0.5–1.0, 1.0–2.0, 2.0–3.0, 3.0–4.0, and 4.0–5.0 m in height. Plots falling within canopy gaps in the forest interior were also noted.

2.3. Statistical analysis

2.3.1. Diversity indices

In order to eliminate any effects caused by sampling at just one transect per site at three sites, we pooled the three transects within each cover type. We considered this approach valid since the site history and edge conditions were similar among all sites and the10 plots sampled at each distance ensured that we captured the community composition. Species richness (R, total number of species per plot), Shannon diversity (H'), and Simpson's Dominance (D) were computed for all plots and then averaged over each distance and for the entire transect (Magurran, 1988). In order to assess how equitable the distribution of species was across the site, evenness ($J=H'/\log(\text{no. of species})$) was also computed across the plots at each distance. Frequency of each species at each distance from the edge and the total estimated understory cover (T) were also computed. We tested for differences in these indices both within a site type, among regions of the transect, and between sites using a Tukey test with a significance value of $\alpha=0.05$.

2.3.2. Functional groupings and depth-of-edge influence determination

Understory species were divided into functional groups based on their abundances along the transect (i.e. distance from the edge), and depth-of-edge influence was determined on a species by species basis. Determination of depth-of-edge influence along a gradient going from one community to another is always arbitrary (Chen et al., 1992, 1996). Various approaches have been used in previous studies to determine depth-of-edge influence values (see Palik and Murphy, 1990; Chen et al., 1992, 1996; Matlack, 1994; Harper, 1999). In this study, the depth-of-edge influence value was defined as the point at which two or more consecutive distances showed a significant ($p=0.05$) irreversible change in species abundance along the transect.

To compare quantitatively the distributions of species along the transects, a band ratio was calculated, where

$$\text{Band ratio} = \frac{\text{mean percent cover of species } i \text{ at distance } d}{\text{mean percent cover of species } i \text{ over the entire transect}}$$

A species band ratio was considered exceptionally high when it was >1.5, indicating that the percent cover at that distance was more than 1.5 times the overall percent cover. A low band ratio was considered <0.50, meaning that it was less than half the overall percent cover. This ratio was used to classify the species into seven different groups:

1. clearcut orientated (greatest abundance in the clearcut);
2. interior orientated (greatest abundance in the forest interior);
3. edge orientated (greatest abundance in the edge zone);
4. clearcut/edge orientated (greatest abundance in the clearcut and edge zone);
5. interior/edge orientated (greatest abundance in the interior and edge zone);
6. rare/single (≤ 5 occurrences);
7. ubiquitous (equal abundance along the transect).

Effects were recorded when there were more than four bands within the clearcut or interior, and two or more bands in the edge zone (from 5 m into clearcut to 5 m into forest interior), that could be considered either high (>1.5) or exceptionally low (<0.50). Alternatively, if the band ratios were nearly one along the entire transect, the species was considered ubiquitous. In order to evaluate visually the species distributions along the transect, the mean percent cover was graphed at each distance for each species group.

Species falling into one of the first five groups were further assessed to determine where a significant decrease into the forest interior (for the edge/clearcut species) or into the clearcut (for the edge/interior species) could be found. For species that were not ubiquitous or rare, the Wilcoxon Rank Sum test using a significance level of 0.05 was employed to determine significant differences in percent cover between pairs of distances. The depth-of-edge influence was then determined by finding two consecutive distances where there was a significant irreversible decrease in cover.

A second method, detrended correspondence analysis (DCA), was implemented using PC-ORD Version 3.0 (McCune and Mefford, 1997) to support the groupings obtained using the abundance ratio methods. Rare and single occurrence species were excluded from the DCA analysis. Those species with high correlations (>0.5) with the distance along axis 1 were plotted against axis 1 scores, allowing us to visualize the species groupings. In addition, DCA was used to classify and graph the plots at each of the sampled distances on the basis of species composition. Correlations with the structural, topographic, and stand composition variables were then calculated and those with high correlations ($|\geq 0.5|$) were overlaid on the graph and compared to the plot scores at different distances.

2.3.3. Multiple regression

Prior to implementing the least-squares regression models, we used Mantel's test to check for spatial autocorrelation along the red pine and jack pine transects using PC-ORD Version 3.0 (McCune and Mefford, 1997). Spatial autocorrelation was thought to have occurred since the plots were located along a transect, and hence not entirely independent. Overall the Mantel Z-statistic was not significant ($p>0.05$), indicating that the samples could be considered independent. Therefore, least-squares regression models could be used without yielding biased estimates.

Multiple regression models were implemented using PROC REG in SAS (SAS Institute, 1990, Version 6.11) with the stepwise option to test the ability to predict H', D, R, and T from all independent variables, including aspect, canopy cover, understory cover class, total estimated grass cover, duff depth, and estimated coarse woody debris. D in the red pine and jack pine transects and H' in the red pine transect were logarithmically transformed in order to account for non-normality. The means of the predictor variables and the diversity indices were computed over distances and edges. Predictor variables in the models obtained from the stepwise regressions were correlated with the response variables and checks for heteroscedasticity were performed in order to verify the accuracy of the models (Weisberg, 1985; Rice, 1995).

3. Results

3.1. Diversity comparisons

Among the 67 species detected, 18 and two species were unique to the jack and red pine stands, respectively (Table 1). Only one exotic species, orange hawkweed (*Hieracium aurantiacum*) was inventoried, and it was found along both the red pine and jack pine transects. Most species were relatively uncommon, occurring in <10% of the sampled plots (Fig. 1). There were nine and five very common species that were found in more than 50% of the plots in the jack and red pine transects, respectively (Figs. 1 and 2).

Species richness (R) was not significantly different between the edge and the clearcut for either patch type. For the red pine, there were significant differences in R from the edge to the interior and from the clearcut and interior, with lower values seen in the interior. Richness was significantly different between the jack pine transects and the red pine transects (Table 2).

Total percent cover (T) was higher in the clearcut, particularly at the red pine sites. The red pine transects showed a distinct increase in estimated coverage at 5 m into the clearcut. The jack pine transects showed an increase at 0 m up to around 15 m into the clearcut

Table 1
Frequency, mean percent cover (when present), functional group classification, and depth of edge influence (DEI) of understory plant species found along a 240 m transect crossing through a clearcut, across an edge, and into a red or jack pine planatation in the Chequamegon National Forest in northern Wisconsin[a]

Code	Species	Jack pine					Red pine				
		Frequency		Mean cover	Functional group	DEI	Frequency		Mean cover	Functional group	DEI
		n	%				*n*	%			
Grasses/sedges											
AGHY	*Agrostis hyemalis*	351	61.6	16.1	U	–	14	2.5	10.8	U	–
CAPE	*Carex pedunculata*	17	3.0	14.2	U	–	1	0.2	3.0	S	–
CAPE2	*Carex pensylvanica*	349	61.2	15.7	E-C	0	273	47.9	9.4	E-C	5
DASP	*Danthonia spicata*	83	14.6	11.2	C	0	211	37.0	14.8	E-C	−5
ORAS	*Oryzopsis asperifolia*	464	81.4	1.7	U	–	312	54.7	10.5	U	10
PAIM	*Panicum lanuginosum*[b]	15	2.6	2.0	E-C	5	5	0.9	2.2	C	−10
PAXA	*Panicum xanthophysum*	68	11.9	2.1	U	–	50	8.8	2.6	U	–
Other herbaceous/woody plants											
ACRU	*Acer rubrum*[c]	93	16.3	5.6	U	–	242	42.5	8.8	U	–
AMEL	*Amelanchier* spp.	214	37.5	9.6	U	–	94	16.5	10.2	U	–
ANMA	*Anaphalis margaritacea*	1	0.2	2.0	S	–	–	–	–	–	–
ANQU	*Anemone quinquifolia*	77	13.5	3.3	U	–	18	3.2	2.1	U	–
ANSP	*Antennaria*sp	2	0.4	2.0	R	–	–	–	–	–	–
APAN	*Apocynum androsaemifolium*	139	24.4	2.2	U	–	88	15.4	2.1	U	–
ARNU	*Aralia nudicaulis*	3	0.5	4.0	R	–	7	1.2	3.2	I	
ARUV	*Arctostaphylos uva-ursi*	78	13.7	12.1	C	15	4	0.7	4.6	E	−10
ASLA	*Aster laevis*	31	5.4	1.7	U	–	53	9.3	2.0	E-C	−15
ASMA	*Aster macrophyllus*	237	41.6	11.2	I	20	142	24.9	5.3	U	–
ASSA	*Aster sagittifolius*	15	2.6	3.9	C	5	–	–	–	–	–
BEPA	*Betula papyrifera*[c]	4	0.7	15.0	R	–	–	–	–	–	–
CARO	*Campanula rotundifolia*	7	1.2	1.1	E-C	5	–	–	–	–	–
CASP	*Cacalia*sp.	1	0.2	1.0	S	–	–	–	–	–	–
CHUM	*Chimaphila umbellata*	9	1.6	2.2	E-I	−5	2	0.4	2.8	R	–
CLBO	*Clintonia borealis*	13	2.3	3.0	I	15	15	2.6	1.7	E-I	
COCA	*Cornus canadensis*	8	1.4	3.4	U	–	–	–	–	–	–
COCO	*Corylus cornuta*	63	11.1	13.6	U	–	68	11.9	27.1	U	–
COMA	*Corallorhiza maculata*	1	0.2	1.0	S	–	–	–	–	–	–
COPE	*Comptonia peregrina*	274	48.1	8.7	U	–	134	23.5	8.6	E-C	30
COSP	*Convolvulus spithamaeus*	37	6.5	3.0	U	–	77	13.5	2.3	U	–
CRSP	*Crataegus* sp.	2	0.4	6.0	R	–	–	–	–	–	–
DILO	*Diervilla lonicera*	203	35.6	7.0	U	–	91	16.0	3.2	E-C	10
EPAN	*Epilobium angustifolium*	5	0.9	1.4	R	–	–	–	–	–	–
EPRE	*Epigaea repens*	38	6.7	5.7	E-I	−30	26	4.6	4.9	U	–
FRVI	*Fragaria virginiana*	90	15.8	3.1	U	–	90	15.8	1.8	U	–
GAPR	*Gaultheria procumbens*	429	75.3	5.8	E-I	−10	462	81.1	5.9	E-I	−15
HIAU	*Hieracium aurantiacum*	30	5.3	4.3	U	–	10	1.8	4.2	U	–
HIFL	*Hieracium florentinum*	14	2.5	1.6	C	−10	–	–	–	–	–
HIER	*Hieracium* sp.	39	6.8	3.1	E-C	5	19	3.3	1.5	R	–
LACA	*Lactuca canadensis*	20	3.5	2.0	U	–	11	1.9	1.7	U	–
LOCA	*Lonicera canadensis*	1	0.2	1.0	S	–	–	–	–	–	–
LYCL	*Lycopodium clavatum*	26	4.6	15.6	I	10	2	0.4	13.5	R	–
LYCO	*Lycopodium complanatum*	–	–	–	–	–	14	2.5	3.9	E-I	−10
LYOB	*Lycopodium obscurum*	24	4.2	3.5	E-I	0	3	0.5	2.7	R	–
MACA	*Maianthemum canadense*	361	63.3	4.7	E-I	−15	328	57.5	2.8	U	–
MELI	*Melampyrem lineare*	45	7.9	1.9	U	–	13	2.3	1.1	U	–
PIBA	*Pinus banksiana*[c]	49	8.6	17.1	E-C	10	50	8.8	18.6	C	−15

Table 1 (*Continued*)

Code	Species	Jack pine					Red pine				
		Frequency		Mean cover	Functional group	DEI	Frequency		Mean cover	Functional group	DEI
		n	%				*n*	%			
PIRE	*Pinus resinosa*[c]	9	1.6	14.1	E-C	0	5	0.9	15.0	E-C	5
POGR	*Populus grandidentata*[c]	3	0.5	4.0	R	–	8	1.4	10.4	U	–
POPA	*Polygala paucifolia*	28	4.9	2.4	U	–	9	1.6	1.6	I	20
POTR	*Potentilla tridentata*	7	1.2	1.7	I	5	–	–	–	–	–
PRAL	*Prenanthes alba*	7	1.2	2.1	E-I	0	3	0.5	1.7	R	–
PRPE	*Prunus pensylvanica*[c]	19	3.3	9.2	U	–	–	–	–	–	–
PRPU	*Prunus pumila*[c]	198	34.7	4.7	U	–	48	8.4	6.3	E-C	10
PRSE	*Prunus serotina*[c]	65	11.4	10.9	E-C	10	29	5.1	9.2	E-I	−20
PRVI	Prunus virginiana[c]	9	1.6	5.1	U	–	–	–	–	–	–
PTAQ	*Pteridium aquilinum*	508	89.1	20.4	U	–	458	80.4	26.8	U	–
QURU	*Quercus rubra*[c]	51	8.9	18.6	E-I	−5	201	35.3	16.1	U	–
ROSA	*Rosa*sp.	14	2.5	3.3	E-I	−10	1	0.2	18.0	S	–
RUAL	*Rubus alleghaniensis*	344	60.4	10.4	U	–	81	14.2	6.8	U	–
SAHU	*Salix humilis*	69	12.1	26.1	E-C	20	–	–	–	–	–
SMRA	*Smilacina racemosa*	2	0.4	3.5	R	–	6	1.1	1.5	U	–
SOHI	*Solidago hispida*	1	0.2	1.0	S	–	–	–	–	–	–
STRO	*Streptopus roseus*	1	0.2	2.0	S	–	–	–	–	–	–
TRBO	*Trientalis borealis*	315	55.3	3.1	E-I	−15	203	35.6	1.6	U	–
VAAN	*Vaccinium angustifolium*	483	84.7	12.0	E-C	5	493	86.5	10.9	E-C	20
VAMY	*Vaccinium myrtilloides*	161	28.2	9.9	E-C	10	124	21.8	10.3	E-C	5
VIOLA	*Viola* sp.	43	7.5	2.3	U	–	63	11.1	2.2	U	–
WAFR	*Waldsteinia fragarioides*	–	–	–	–	–	6	1.1	6.8	C	−10

[a] Codes are those referred to in Figs. 2 and 3; species considered very common had a frequency ≥285. Nomenclature follows that of Gleason and Cronquist (1991). Group codes — R: rare (2–5 occurences); S: single occurrence; U: ubiquitous, E: edge orientated; I: interior orientated; E-I: edge-interior orientated; C: clearcut orientated; E-C: edge-clearcut orientated.

[b] Var. implicatum.

[c] Seedlings and saplings combined.

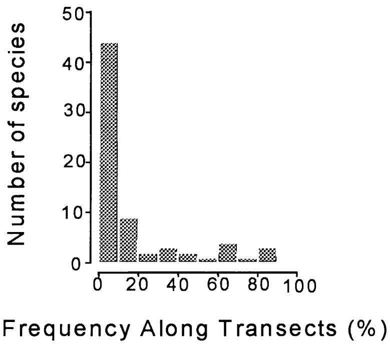

Fig. 1. Frequency distribution of understory plants along a 240 m transect crossing through a clearcut to the adjacent red and jack pine plantations. Of the 67 species inventoried, most fell into <10% of the 1140 plots sampled.

(Appendix A). *T* was also significantly different between the red pine and jack pine (Table 2). The jack pine canopy was generally less dense than the red pine canopy, and more canopy gaps were noted within the jack pine stands. The mean percent canopy cover within the jack pine interior was 62% while within the red pine interior the mean was 87% (Appendix A).

H' and D were also significantly different between the red and jack pine stands. However, within the jack pine transects, there was no significant difference between the clearcut/interior, edge/clearcut, or edge/interior for D. There was a difference in the edge/interior and edge/clearcut in terms of H' at the jack pine stands. The red pine exhibited no difference between the edge/clearcut for either H' or D, but did show differences between the edge/interior for

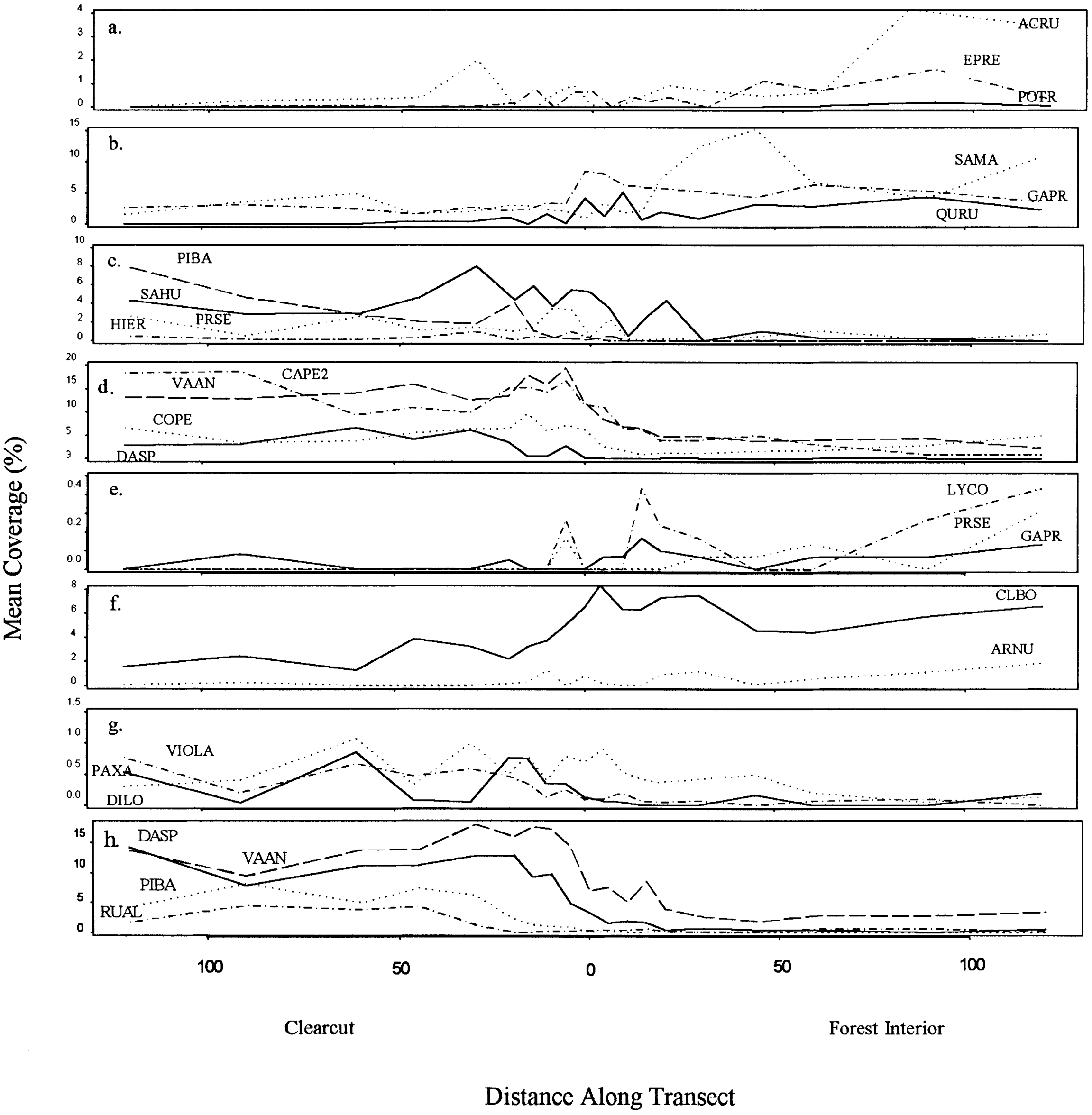

Fig. 2. Distributions of understory species groups found in the jack and red pine stands using the groups obtained from DCA ordinations. Graphs (a–d) depict jack pine stands where graphs (a) and (b) illustrate edge/interior species of lower and higher abundances and graphs (c) and (d) illustrate edge/clearcut species of higher and lower abundances; graphs (e–h) depict red pine stands with (e) and (f) illustrating edge/interior species of lower and higher abundances and (g) and (h) illustrating edge/clearcut species of higher and lower abundances. See Table 1 for a translation of species abbreviations.

these indices (Table 2). Evenness was significantly different between the red pine and jack pine stands, but was not significantly different between the edge/clearcut, edge/interior, or clearcut/interior for either stand type (Table 2).

3.2. Functional groupings and depth-of-edge influence

Functional groupings obtained using abundance band ratio calculations and DCA were similar

Table 2
Diversity indices and estimated cover values for red pine and jack pine sites[a]

	Mean	Range	Significance of p-values			
			Clearcut/interior	Edge/interior	Edge/clearcut	Red pine/jack pine
Shannon diversity (H')						
Jack pine	0.86	0.78–0.90	No	Yes	Yes	Yes
Red pine	0.68	0.57–0.74	No	Yes	No	
Richness (R)						
Jack pine	11.2	10.2–12.2	No	No	No	Yes
Red pine	8.1	6.1–9.1	Yes	Yes	No	
Simpson's dominance (D)						
Jack pine	6.3	1.4–10.9	No	No	No	Yes
Red pine	3.9	1.1–8.6	Yes	Yes	No	
Evenness (E)						
Jack pine	0.83	0.76–0.86	No	No	No	Yes
Red pine	0.77	0.73–0.81	No	No	No	
Total coverage (T, %)						
Jack pine	110.9	63–165	No	No	No	Yes
Red pine	79.5	16–135	Yes	Yes	Yes	

[a] Tukey tests were used to make comparisons, and significance is at the 0.05 level. Edge comparisons were made using the edge zone defined from 5 m into the clearcut to 5 m into the forest interior.

(Table 1, Fig. 3). There were 25 and 23 species classified as ubiquitous in the jack and red pine stands, respectively. At the jack pine edge there were 12 species grouped as either edge/clearcut or clearcut species, and 13 edge/interior species. Fourteen species were rare/single occurrence. For the red pine edges, there were 11 edge/clearcut species, five edge/interior species, and eight species that were rare/single occurrence (Table 1).

The largest depth-of-edge influence for an edge-forest species was 30 m into the clearcut for *Epigea repens* at the jack pine sites. The largest depth-of-edge influence for an edge-clearcut species was 30 m into the forest interior for *Comptonia peregrina* at the red pine sites. Although there were no species found only at the edge and species richness did not change significantly along any transects sampled in the jack pine, there was a change in species composition sampled from 20 m into the forest and 20 m into the clearcut for both transects. Notably, five species in the jack pine stand showed an irreversible shift in abundance directly at the edge (Table 1).

Of the nine very common species at the jack pine sites, three (*Trientalis borealis*, *Gaultheria procumbens*, and *Maianthemum candadense*) showed an edge-interior preference, one (*Vaccinium angustifolium*) showed an edge-clearcut preference, and the remaining five were ubiquitous. At the red pine stands, one very common species (*G. procumbens*) was an edge-interior species, one preferred the edge-clearcut (*V. angustifolium*), and three were ubiquitous.

Species found at both edge types did not always fall into the same functional groups. Notably, *Diervilla lonicera* was ubiquitous in the jack pine sites, but in the red pine sites it was more prevalent in the edge/clearcut, showing a significant decrease at 10 m into the forest. *Aster laevis*, a species often found in open, dry, and disturbed sites, showed an edge/clearcut preference in the red pine transects, but no preference in the jack pine transects (Table 1 and Fig. 3a). Similarly, *Aster macrophyllus*, a forest plant, was found primarily in the jack pine interior, but was ubiquitous at the red pine sites. However, *V. angustifolium* and *Vaccinium myrtilloides* were both classified as edge/clearcut species with depth-of-edge influences that were similar in both the red and jack pine stands (Table 1 and Fig. 3a and b).

DCA ordinations also indicated that, for both the red and jack pine transects, the clearcut to interior sampling distances could be separated into a distinct

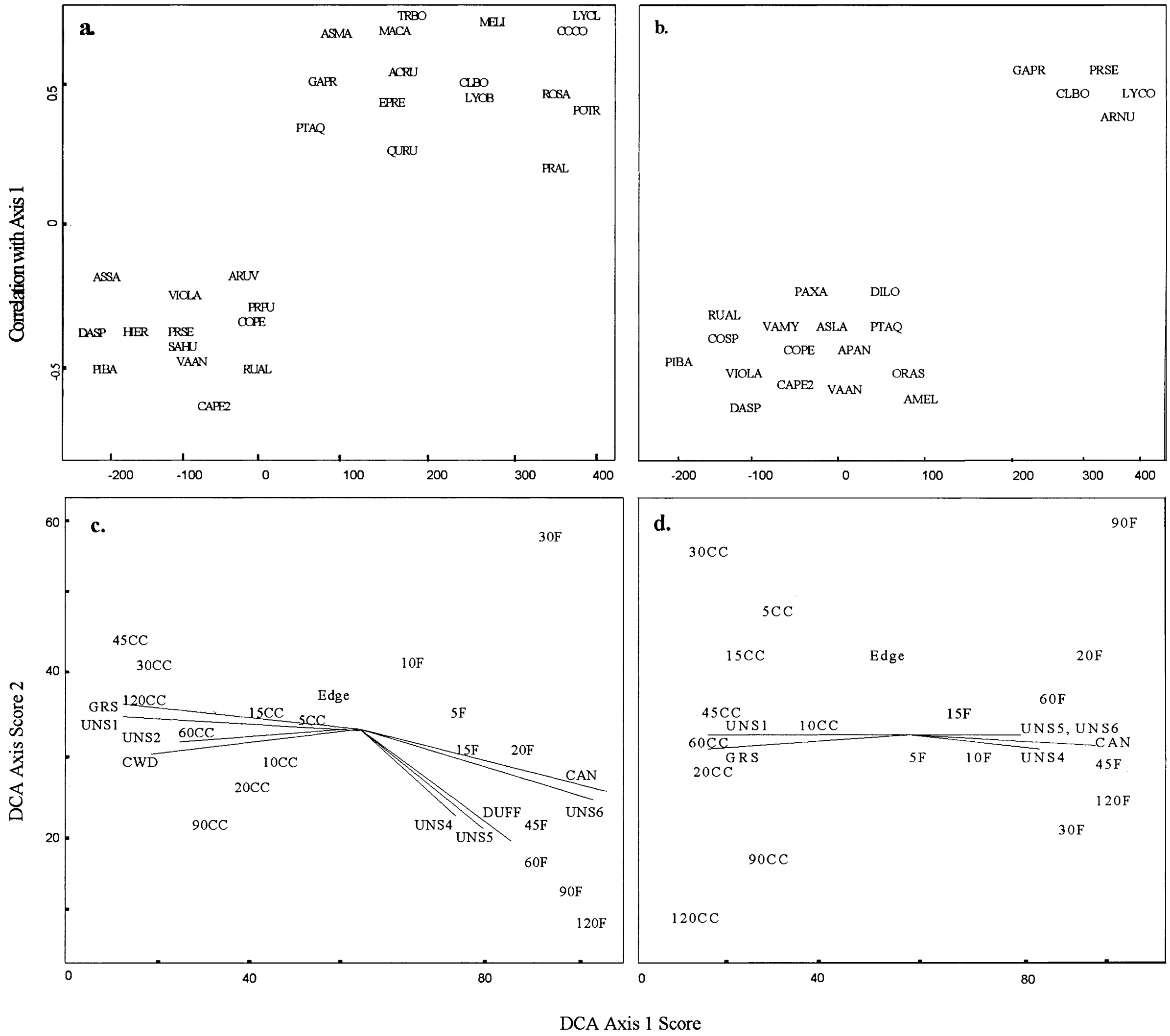

Fig. 3. DCA classification of plant species occurring in jack pine (a) and red pine (b), and DCA classification and high correlations (|≥0.5|) with the structural, topographic, and stand composition variables for red pine (c) and jack pine (d) of plot locations along the 240 m transect going across the clearcut (CC) to the adjacent forest interior (F). Understory cover classes were estimated by percent total understory from 0–0.5 m (UNS1), 0.5–1.0 m (UNS2), 1.0–2.0 m (UNS3), 2.0–3.0 m (UNS4), 3.0–4.0 m (UNS5), and 4.0–5.0 m (UNS6) in height. CAN: percent estimated canopy cover; DUFF: duff depth; GRS: estimated grass cover. See Table 1 for a translation of species abbreviations.

gradient. The clearcut plots fell onto the lower end of the DCA diagram, edge plots fell near the middle, and interior plots were generally a bit higher along DCA axis 2 (Fig. 3c and d). Correlations with the structural, topographic, and stand composition variables showed that in the red pine sites there was a strong association between the clearcut plots and estimated grass cover, coarse woody debris, and estimated understory cover between 0–0.5 and 0.5–1.0 m. For the forest interior plots, strong associations were seen for duff depth, canopy cover, and estimated understory cover between 2.0–3.0, 3.0–4.0, and 4.0–5.0 m (Fig. 3c). In the jack pine transects, strong associations with the clearcut plots existed for estimated grass cover and estimated understory cover between 0–0.5 m. Canopy cover and estimated understory cover between 2.0–3.0, 3.0–4.0, and 4.0–5.0 m were strongly associated with the jack pine forest interior.

Table 3
Least squares multiple regression models predicting diversity indices or total plot cover from topographic, stand structure, and composition variables[a]

	F	R^2
Red pine transects		
$\log(D)=0.70+0.00029\mathrm{ASP}+0.0067\mathrm{SLP}-0.0023\mathrm{GRS}+0.00464\mathrm{CWD}$	4.5	0.26
$R=3.74+0.006\mathrm{ASP}+0.035\mathrm{UNS1}+0.042\mathrm{UNS2}-0.175\mathrm{CWD}$	27.6	0.68
$\log(H')=-0.28+0.00019\mathrm{ASP}+0.001\mathrm{UNS1}+0.0007\mathrm{UNS2}-0.0057\mathrm{CWD}$	16.2	0.55
$T=-28.99+0.129\mathrm{ASP}+1.14\mathrm{CAN}+0.699\mathrm{UNS2}-1.39\mathrm{UNS4}$	34.5	0.73
Jack pine transects		
$\log(D)=0.76-0.001\mathrm{CAN}-0.002\mathrm{UNS2}+0.004\mathrm{UNS3}+0.01\mathrm{UNS6}+0.01\mathrm{CWD}$	7.3	0.41
$R=12.38-0.26\mathrm{SLP}-0.33\mathrm{DUF}+0.04\mathrm{UNS2}$	12.5	0.41
$H'=0.83-0.009\mathrm{SLP}+0.001\mathrm{UNS1}+0.002\mathrm{UNS3}-0.005\mathrm{UNS4}$	7.9	0.38
$T=26.95-2.47\mathrm{SLP}-0.32\mathrm{CAN}+0.70\mathrm{UNS1}+1.58\mathrm{UNS2}$	32.1	0.71

[a] D: Simpson's dominance; R: richness; H': Shannon diversity; T: total estimated cover (%); ASP: aspect (□); SLP: slope (%); GRS: estimated grass cover (%); CWD: coarse woody debris (%); CAN: canopy cover (%); total understory (%) from 0–0.5 m (UNS1), 0.5–1.0 m (UNS2), 1.0–2.0 m (UNS3), 2.0–3.0 m (UNS4), 3.0–4.0 m (UNS5), and 4.0–5.0 m (UNS6) in height. All models are significant at p□.003.

3.3. Multiple regression

For the red pine transects, the most consistent predictors of diversity (H', D) and T were aspect, percent of understory cover 5–10 m, and percent coarse woody debris cover. Coarse woody debris cover was negatively correlated with richness and the log of H', but positively correlated with the log of D. For the jack pine transects the most consistent predictors were slope and percent of understory cover 5–1.0 m, coarse woody debris was again positively correlated with the log of D. At the red pine transects, 26, 68, 55, and 73% of the variation in D, R, H' and T, respectively, was explained by the models. For the jack pine transects, 41, 41, 38 and 71%, of the variation in D, R, H', and T, respectively, was explained by the models. In the jack and red pine transects the highest R^2 values (0.71 and 0.73, respectively) were obtained using total estimated cover as the predictor (Table 3).

4. Discussion

4.1. Estimated depth-of-edge influence and species distribution

Our results suggest that a depth-of-edge influence value of around 30 m should be considered when managing landscapes containing these conifer forest-clearcut edges. We emphasize that this estimate is based primarily on understory vegetation patterns, and does not take into account the edaphic or microclimatic features of these ecosystems. Our maximum depth-of-edge influence of 30 m differs slightly from other studies that have determined a maximum depth-of-edge influence from 0 to 137 m (Table 4). This may be caused by differences in, for example, sampling design, geographic region, time of year sampled, age of edge, edge type, or orientation of edge (Table 4). For example, Fraver (1994, Table 4) found a 60 m depth-of-edge influence at 50-year-old agricultural edges in NC, USA. Renhorn et al. (1997, Table 4) documented a 100 m depth-of-edge influence at clearcut edges 15 years of age in northeastern Sweden.

Excluding extremely low-abundance and ubiquitous species groups, the distribution of plant species across the clearcut to the forest interior follows seven different abundance patterns (Fig. 4). For example, *Clintonia borealis*, an edge/interior species within the red pine stands, showed a peak at 5 m from the edge (Fig. 2f), corresponding to line 7 in Fig. 4b. *Danthonia spicata*, an edge/clearcut species within the jack pine stands, showed a peak at 20 m from the edge (Fig. 2h), corresponding to line 5 in Fig. 4b. We can generalize the pattern in terms of edge and interior species (or, alternatively, clearcut species, the mirror image of interior species). The edge species show a distinct increase near the edge but exhibit several patterns (Fig. 2). Murcia (1995) hypothesized that the edge

Table 4
Summary of previous selected studies on understory plant species across edges within northern temperate forests

Study	Locality	Fragment size	Edge type	Age (years)	Edge effect on understory species	DEI[a]	Length of transect
Brosofske et al. (1999)	Northern Wisconsin, USA	15400 ha of pine barrens	RD	Not specified	Plant species distribution and diversity varied with the type and usage of the road	Not specified	3575 m in pine barrens landscape
Chen et al. (1992)	S. Washington, Central Oregon, USA	Not specified	CC	10–15	Certain shade-intolerant seedlings showed edge preference while others did not	16–137 m	From 0–240 m into forest
Esseen and Renhorn (1998)	Northwestern Sweden	20×50 km sq.	CC	0.5–16	Lichen abundance lower at edge and varied with age of the edge	up to 50 m	From 5–100 m into forest
Fraver (1994)	North Carolina, USA	Not specified	AG	≥50	28 edge-restricted species, no interior-restricted species, 11 edge-orientated species	up to 60 m	100 m into forest
Harper (1999)	Alberta, Canada	Not specified	CC	1–16	Over all years, the most significant changes in forest structure and composition occurred in <20 m of the edge	From 0 to 60 m, depending on the species	200 m into the forest from the edge
Jules et al. (1999)	Northwest California and southwest Oregon, USA	Generally 10–20 ha	CC	18–26	Forest-interior response most common, 12 forest-restricted species, 6 clearcut restricted, 21 clearcut orientated	from 0 to 60 m, depending on the species	60 m into forest and 30 m into clearcut
Matlack (1994)	Delaware, Pennsylvania, USA	4–100 ha	AG	1.5 to >114	15 species distributed more commonly at forest edge	Up to 40 m	From 0–40 m into forest
Pyle and Chen (1998)	S. Washington, Central Oregon, USA	Not specified	CC	23	Six exotic edge-orientated species, 13 forest-orientated species, no forest or edge restricted species	0–120 m	From 0–240 m into forest
Palik and Murphy (1990)	Southern Michigan, USA	2.7–4.7 ha	AG	≥50	Edge effect associated with the disturbance history of the sites	up to 35 m	50 m into forest
Reed et al. (1996)	Southeastern Wyoming, USA	30, 123 ha (size of national forest)	RD	Not specified	13–25% of vegetation becomes road edge habitat	100 m	No transect
Renhorn et al. (1997)	Northeastern Sweden	24 ha, 400 minimum width	CC	15	No evidence of decreased lichen growth near edge	100 m	None

[a] DEI: depth-of-edge influence pertaining to understory plant species; 0 means no DEI. Edge types are AG: agricultural; CC: clearcut; RD: road.

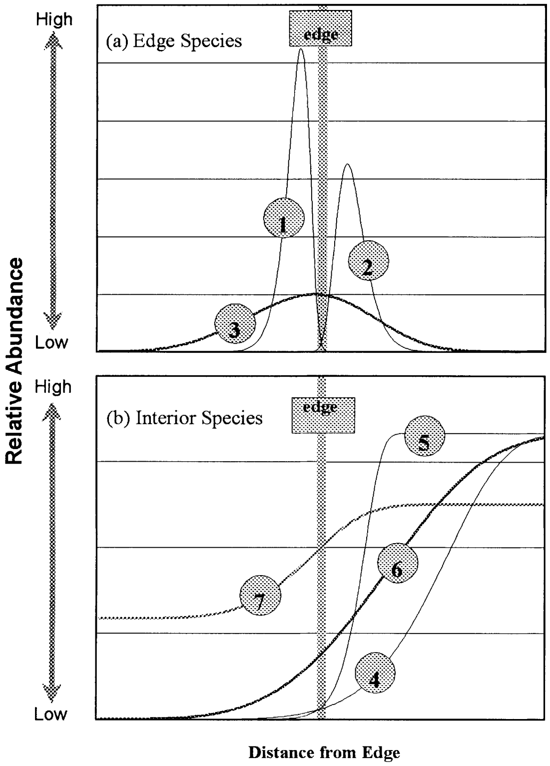

Fig. 4. Synthesis model for species abundance across edges. Lines (1–3) in (a) depict three typical distribution patterns of 'edge species', and lines (4–7) in (b) illustrate four typical patterns of 'interior species'. Note that 'clearcut species' are the mirror image of the 'interior species'.

effects are not always symmetric or monotonic around the edge (also see Chen et al., 1996). Our results substantiate this hypothesis since many of the patterns did not follow a bell-shape (3 in Fig. 4a), but were generally more asymmetric, i.e. stronger edge effects on one side than the other (1 and 2 in Fig. 4a). The depth-of-edge influence value for the two sides of the edge may also differ significantly depending on community type, composition, and the variable or species of concern. Some species showed no clear response to the edge, similar to a ubiquitous species. Murcia (1995) suggested that no pattern could indicate two interacting edge effects that negate each other, causing no visible overall effect in the understory species distribution.

Edges can also produce several patterns in the distribution of interior species (Fig. 4b). In general, the species abundance increases with distance into the forest (or the clearcut; 4 in Fig. 4b) but the rate of increase may vary among species (i.e. 4 versus 5 in Fig. 4b). For example, in the red pine stands, abundance of the clearcut/edge species *D. spicata* and *V. angustifolium* increased sharply while that of *P. banksiana* seedlings and *Rubus alleghaniensis* increased at a more moderate rate (Fig. 2h). Interior species that can extend their distribution into the adjacent community may exhibit another pattern (6 and 7 in Fig. 4b); whether they maintain a certain abundance (7 in Fig. 4b) or diminish (6 in Fig. 4b) is a function of species. For instance, in the jack pine stands *C. peregrina* demonstrated a distinct clearcut preference, but was also present in lower abundances within the forest interior, but *D. spicata* was only found within the clearcut. Edge effects in terms of an increase in exotic species were minimal, suggesting that these younger, relatively isolated, north-facing forest fragments are better able to resist exotic invasion.

Diversity, as measured by H' versus D, gave slightly different results for comparisons between the clearcut/interior, edge/interior, and edge/clearcut (Table 2). H' is sensitive to rare species, but D is not; therefore, D may give a more correct estimate of diversity when rare species are included in the data (Pitkanen, 1998). There were 14 rare/single occurrences of species in the jack pine sites but only eight in the red pine sites. This implies that H' should be examined in concert with D to highlight patterns in rare species that might otherwise be missed. Furthermore, R and D should also be examined together. A high species richness and low dominance indicates that when numerous species occur together, none dominants, thereby preventing competitive exclusion.

4.2. Red pine/jack pine differences

The red pine and jack pine transects were significantly different in terms of understory species composition as evidenced by the significant differences in H', D, R, E, and T between the two site types (Table 2). Due to the less dense jack pine canopy, greater light levels reaching the jack pine stands could allow for the increased understory growth of more opportunistic shade-intolerant species. Furthermore, the dense blanket of red pine needles covering the red pine interiors may cause repression of all but the most resistant species. This was evidenced by the high percentage of woodier species, such as *Acer rubrum* seedlings, *Quercus rubra* seedlings, and *G. procumbens* found at the red pine transects (Table 1). A previous study found no significant differences in site or soil variables (e.g. soil pH, moisture, carbon and nitrogen content, total organic matter, litter, or coarse woody debris) between jack and red pine plantation types in this landscape (Brosofske et al., 2000). These results indicate that the differences we see between the understory plant distributions were more likely caused by plantation effects and not site dissimilarities.

The depth-of-edge influence at the red and jack pine transects was similar, but as Palik and Murphy (1990) suggested, edge effects could be expressed in the interior forest following disturbance events, such as multiple tree falls. This would have the effect of increasing the depth-of-edge influence and edge effect within the jack pine interior. Clearly, future efforts in field and modeling exercises are needed to address such multiple edge effects (Zheng and Chen, 2000) and related measurements (e.g. depth-of-edge influence).

4.3. Multiple regression implications

Many of the structural, compositional, and topographic variables measured played some role in predicting species diversity as measured by richness, Shannon diversity, or Simpson's dominance. In particular, slope, aspect, coarse woody debris, and several levels of estimated understory cover by height played important roles in these predictions. Total estimated grass cover was not a significant factor in predicting species richness. This is contrary to the expected result since the increased grass cover normally seen within clearcuts suggests high dominance as plots are then covered by just a few grass species. It was also surprising to note that coarse woody debris showed a positive correlation with the logarithm of D since a large percentage of coarse woody debris, also noted within the clearcuts, excludes species from utilizing this space. Large amounts of coarse woody debris may be one of the few sources of moisture and shade for regenerating understory in otherwise harsh clearcut environments. Finally, given that aspect was measured on a fine scale, e.g. within each 1 m×1 m plot, this yielded a wide range of values, and may potentially limit the usefulness of this variable to predict diversity within this landscape. Given the significance of certain model parameters, these results demonstrate that it may be possible to manage these portions of the northern Chequamegon National Forest for biodiversity based on certain topographic, compositional, and structural variables. However, these models may not be generalizable for all red or jack pine sites in the Lake States since they were developed specifically for these sites. It would be interesting to obtain additional data from other locations in the region to test the general applicability of our models.

4.4. Forest management

The ecology of the managed system is affected by management practices, and recent Forest Service initiatives have placed an emphasis on biotic diversity and ecosystem management (USDA, 1994). Thus, the basis of forest management should include a comprehension of the underlying plant diversity patterns and forest ecosystem processes. Forest managers should retain depth-of-edge influence information when making harvest plans since the functional edge may not correspond to the edge of the forest as depicted on a map (Chen et al., 1996). Our results suggest that a 30 m buffer zone around the north-facing edges of red and jack pine plantation fragments would maintain a forest interior environment, which is required for maintenance of interior understory plant species.

However, managers may need to plan for other types of patch adjacencies. A pine plantation surrounded on all sides by clearcuts may be more subject to disturbances, such as tree blowdown or fire than one surrounded by different patch types, such as wetlands or less contrasting forest types. Furthermore, south, east or west-facing edges may have a greater depth-of-edge influence than north-facing edges (Palik and Murphy, 1990; Chen et al., 1995) indicating that a buffer of 30 m may not be adequate for an edge of different orientation. In addition, the edge contrast may mitigate edge effect; for example retention cuts may moderate the edge effect (Franklin, 1992). Finally, patch types that are more 'natural' than plantations may have different edge effects due to a different understory composition.

Managers should also realize that even species within a functional group exhibit highly variable patterns across the edge. If the management goal is to preserve species diversity from edge to forest interior then a buffer zone larger than the estimated depth-of-edge influence may need to be planned since species within a functional group have varying depth-of-edge influences and sampling schemes may not always capture all species. In addition, it is difficult to reach a conclusion regarding the depth-of-edge influence of rare species due to their low numbers, but these may be of a concern to land managers. On the other hand, if the management goal is to preserve 90% of the edge to forest interior understory diversity, then a buffer zone smaller than the estimated depth-of-edge influence may be sufficient.

5. Conclusions

We found that the understory species sampled in this study had unique responses to fragmentation, and their distributions often differed between the red pine and the jack pine edges. Vegetation responses were noted going across the clearcut to interior gradient, and a synthesis model was presented to describe the observed abundance patterns. A depth-of-edge influence of 30 m may be sufficient in order to preserve understory plant diversity at these north-facing sites, but further research is needed to estimate the depth-of-edge influence at clearcut-coniferous edges of other orientations. Furthermore, relatively little is known about the life histories and habitat requirements for many of the understory species encountered in this study, and the preservation of diversity within these clearcut-coniferous forest edges is also dependent on acquiring this information.

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Appendix A.

Values of topographic, stand compositional, and structural variables averaged over the three edges by distance along the transect for jack pine/red pine. Negative numbers represent distance from the edge (0 m) into the clearcut and positive numbers represent distance from the edge into the clearcut

							Percent estimated understory coverage by height (m)					
Distance from edge	Aspect (°)	Slope (%)	Canopy cover (%)	Duff (cm)	Grass cover (%)	CWD (%)	<0.5	0.5–1.0	1.0–2.0	2.0–3.0	3.0–4.0	4.0–5.0
−120	200.5/142.2	5.8/4.9	23.5/4.4	2.0/3.1	32.4/38.9	3.8/4.9	87.1/95.5	48.4/31.6	11.1/15.2	6.0/5.5	2.4/0.8	1.4/0
−90	201.9/189.2	7.1/5.3	23.2/1.6	2.3/3.1	19.5/43.3	12.5/3.7	71.1/94.0	61.1/21.2	13.1/10.2	3.8/2.3	1.7/1.0	0.9/0
−60	197.4/184.8	7.7/5.5	20.9/3.4	2.3/3.7	27.8/32.8	9.9/4.3	80.6/95.3	60.9/16.3	11.1/3.6	5.6/1.7	3.1/0.3	1.5/0
−45	186.1/165.7	6.5/5.6	22.8/1.2	2.1/2.4	30.2/33.7	7.1/6.0	90.6/96.0	48.5/22.3	7.8/4.7	4.3/2.3	2.1/0.5	0.9/0.2
−30	204.8/188.9	6.5/7.0	16.5/2.6	1.9/4.3	28.7/33.0	6.3/3.8	88.7/97.0	48.6/21.9	8.5/4.8	4.5/3.2	1.9/0.5	0.9/0.2
−20	266.3/199.7	5.4/5.5	16.4/3.0	2.5/4.0	26.9/37.5	10.5/6.5	71.9/94.0	56.3/20.4	20.3/6.3	6.5/2.9	3.1/0.5	1.6/0
−15	263.4/200.6	4.5/6.0	23.4/5.1	2.6/2.4	23.6/38.5	8.0/4.1	78.6/96.8	56.6/32.0	18.3/7.8	7.5/1.0	2.9/0.5	1.4/0.5
−10	274.9/214.5	4.0/5.3	28.8/5.6	2.1/2.6	22.3/37.5	7.3/8.9	73.3/95.8	43.7/33.2	19.3/12.8	9.4/4.0	4.6/3.3	2.5/0.7
−5	271.2/172.6	3.9/5.0	25.9/15.6	2.1/2.9	16.9/43.7	7.8/2.4	86.3/98.8	43.8/34.4	13.3/11.3	3.8/2.3	1.3/1.0	0.8/1.2
0	277.8/149.2	3.3/4.4	55.0/38.2	2.2/2.9	19.3/30.0	7.2/9.0	72.5/89.8	31.0/25.2	16.4/9.3	8.0/2.7	5.1/1.3	5.4/1.3
5	267.6/146.4	4.3/5.3	72.0/46.4	2.4/3.8	11.2/24.8	3.5/12	59.4/79.1	25.3/25.2	9.2/12.8	7.7/5.2	6.0/2.8	5.9/2.2
10	266.9/130.8	3.6/5.2	80.3/54.4	2.6/3.9	7.7/26.1	2.5/8.2	43.8/92.7	17.7/32.0	5.2/8.0	4.0/4.8	2.7/4.0	3.6/3.3
15	281.6/134.3	3.5/5.3	80.4/57.6	2.8/4.0	8.0/27.8	2.4/11.4	42.6/89.5	25.1/33.7	6.7/10.5	8.5/7.3	3.8/4.3	3.4/1.3
20	239.7/126.2	3.6/4.3	88.2/64.7	2.9/3.6	7.1/25.7	2.4/13.6	36.9/80.4	22.8/34.2	7.3/16.8	7.3/6.2	5.8/1.5	8.5/0.2
30	211.0/155.4	3.9/4.4	93.0/63.5	2.6/3.5	7.9/28.7	2.4/5.6	35.2/84.3	18.4/21.4	8.5/10.4	8.3/4.1	6.2/1.1	9.4/0.9
45	195.1/185.0	4.1/5.1	91.6/64.7	3.0/3.6	6.1/26.4	4.0/6.9	35.2/86.5	23.0/34.3	9.3/14.3	6.6/7.3	3.6/2.0	2.6/1.8
60	196.6/183.3	3.9/5.8	90.7/64.0	3.0/3.4	4.3/30.1	1.3/4.6	37.3/85.9	31.8/37.6	9.5/16.9	7.3/5.7	6.1/1.6	6.3/1.3
90	226.1/263.6	5.0/5.4	93.2/73.8	3.1/3.7	4.5/16.4	3.1/5.0	36.0/65.5	24.4/28.3	12.9/19.0	11.4/10.2	9.7/8.0	8.6/5.2
120	131.7/256.6	5.5/4.5	91.6/71.6	2.9/4.0	3.2/18.6	1.3/7.8	39.2/70.8	32.6/41.5	14.3/12.4	12.4/9.0	11.7/6.5	13.7/5.1

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