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First-year impacts of shelterwood logging on understory vegetation in an old-growth pine stand in central Ontario, Canada

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Summary

There is evidence in the literature that a variety of logging practices may result in significant short and long-term changes to vegetation in the forest understory, however, these changes are still largely unknown for many forest types. The objective of this study was to determine the short-term effects of shelterwood logging on tree and non-arboreal plant species composition and diversity in both the understory and sapling strata within the Owain Lake Stand of old-growth red and eastern white pine located in Temagami, Ontario. The most significant changes were increases of white birch (800%), red maple (363%) and bracken fern (110%) in the understory. The most significant decreases within the understory occurred in mosses and liverworts (110%), Canada mayflower (49%) and starflower (28%). Bracken fern, red maple, and bush honeysuckle were the three most abundant species in the post-harvest understory plant community and will probably increase in their abundance under the present disturbed condition. A second shelterwood cut in 20 to 40 years may further facilitate an increase in these three species primarily by increasing light levels at the forest floor. All three species are very vigorous and are likely to dominate the forest understory until the upper canopy closes resulting in decreased light intensity at the forest floor.

Keywords: old-growth red and eastern white pine forest, understory vegetation, landscape ecology, forest conservation, Temagami

Introduction

As an applied branch of ecology (Kimmins 1973; Wilson 1993), the field of forestry has largely ignored the impacts of logging on plants other than trees (e.g. Johnson *et al.* 1993; Bratton 1994; Halpern & Spies 1995). Of late, however, numerous government policy directives in Ontario have called for the assessment of forestry impacts on all levels of biodiversity and for an increase in biodiversity protection. The same holds true for the other provinces of Canada (Attridge 1996) and for many other countries throughout the world (Myers 1995; Noble & Dirzo 1997). In Ontario, these directives include but are not limited to: A Comprehensive Forest Policy Framework for Ontario (Ontario Forest Policy Panel 1993), the Crown Forest Sustainability Act (Government of Ontario 1994), The Conservation Strategy for Old-Growth Forest Ecosystems in Ontario (Ontario Old Growth Forests Policy Advisory Committee 1994), the Class Environmental Assessment for Timber Management (Ontario Environmental Assessment Board 1994), A Conservation Strategy for Old-Growth Red and White Pine Forest Ecosystems for Ontario (Ontario Ministry of Natural Resources 1995), and the Report of the Comprehensive Planning Council on Land Use for the Temagami Comprehensive Planning Area (Temagami Comprehensive Planning Council 1996).

Despite these policy directives and despite silvicultural policy stating that 'forest managers must be aware of the consequences of silvicultural practices on stand species composition' (Ontario Ministry of Natural Resources 1997, section 10, p. 9–10), silvicultural prescriptions for red pine (*Pinus resinosa*) and eastern white pine (*Pinus strobus*) forests do not take into account the impacts of logging on non-arboreal plant communities. The only consideration given to non-arboreal plants in the silvicultural prescriptions addresses a few shrub and tall herbaceous plant species in the context of their potential for competition with regenerating tree species and as producers of seed and fruit for consumption by animal wildlife (Ontario Ministry of Natural Resources 1997).

The lack of attention to the impacts of silvicultural operations in Ontario may in part be due to a general opinion amongst scientists as well as foresters within the Ontario Ministry of Natural Resources (OMNR) that 'appropriate harvesting techniques [including shelterwood] will not result in irreversible harm to "old-growth" ecosystems in general' (Crins 1996, p. 6). In contrast, however, there is substantial evidence that logging does result in significant changes, including those that affect the forest understory and that for many forest types, including red and eastern white pine forests, these changes are still largely unknown (Duffy 1993; Johnson *et al.* 1993; Bratton 1994; Matlock 1994). In addition, it is now generally accepted that older, pristine forests are more biologically diverse than younger, logged forests and therefore provide unique ecological value (Spies 1994). The objective of this study was to identify and charac-

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terize the initial effects of shelterwood logging on tree and non-arboreal plant species composition and diversity in both the understory and sapling strata within an old-growth red and eastern white pine forest stand. Only the initial, short-term effects were addressed due to constraints of available resources, primarily funding, in carrying out additional long-term monitoring. This forest type has been identified as an endangered ecosystem; < 2% of the original area remains (Quinby 1993; Noss *et al.* 1995; May 1998), and of what remains throughout eastern North America, most is located in central Ontario.

Study area

The area studied is located in the south-east corner of Hebert Township and crosses into the north-east corner of Burnaby Township bordering the west side of the Ottawa River approximately 72 km due north of North Bay, central Ontario, Canada. It has been named the 'Owain Lake Stand' after the largest lake located within the area. It was chosen for study because it was a prime example of old-growth red and eastern white pine forest in Ontario and because it was the subject of debate regarding its suitability for logging. The aggregate stand is about 1400 ha in size and is composed of numerous smaller pine stands. According to the Forest Resource Inventory Maps (Ontario Ministry of Natural Resources 1991) for the area, red and eastern white pine together made up 60% of the forest species composition. For the logged portion, red and eastern white pine represented about 33% of the species composition (Table 1). jack pine (25.5%) and white birch (18.5%) also contributed high proportions to the forest composition of the logged portion. The less common tree taxa included black spruce (8.3%), poplar (7.9%), white spruce (4.1%), and tolerant hardwoods (2.6%). Government logging records indicate that prior to 1996, there had been no logging in the 1400 ha Owain Lake Stand, and aside from a few stumps, a rapid field reconnaissance revealed no evidence of commercial logging. Shelterwood logging (approximately 50% basal area reduction) began in September 1996 and by the end of the year, 320 ha had been logged. The unlogged portion of the Owain Lake Stand is still unprotected despite evidence indicating that the stand provides a unique contribution to regional ecological representation (Quinby 1996*b*).

Methods

The understory and sapling strata in the logged area of the Owain Lake Stand were sampled in July 1996, two months prior to first-cut shelterwood logging, and in August of 1997, approximately eight months after logging. Three to four of these post-logging months fell within the growing season. In the forested landscape of the Temagami region, the habitat gradient is represented primarily by variation in topography. In general, along the gradient from hilltops down slopes and into valleys and finally into the riparian zone, (a) soil depth increases, (b) soil moisture increases, (c) soil nutrient concentrations increase, (d) light at the forest floor decreases, (e) wind exposure decreases, (f) soil and air temperatures decrease, and (g) fire frequency and intensity decreases (Anderson *et al.* 1969; Bratton 1976; Oke 1978; Pregitzer & Barnes 1982; Beatty 1984; Brady 1984; Fralish 1988; Baldwin *et al.* 1990). For this study, the variety of upland forest habitat types as indicated by slope positions (topography) was

Table 1 Tree species composition of the stands prior to logging in the Owain Lake old-growth pine area (upper value for species biomass is total wood volume [m^3] and lower value is the % of the total volume; Pw = white pine, Pr = red pine, Pj = jack pine, Sb = black spruce, Sw = white spruce, Po = poplar, Bw = white birch, Th = tolerant hardwoods; FRI = forest resource inventory; adapted from Ontario Ministry of Natural Resources 1997).

FRI stand no.	*Stand area (ha)*	*Species biomass*								*Stand biomass*	
		Pw	*Pr*	*Pj*	*Sb*	*Sw*	*Po*	*Bw*	*Th*	*(total m^3)*	*(m^3/ha)*
2649	106	1727	1076	2700	0	0	0	2811	0	8314	78.4
		20.8	12.9	32.5				33.8			
3034	36	458	384	0	814	407	415	0	254	2732	75.9
		16.8	14.0		29.8	14.9	15.2		9.3		
3139	60	584	490	0	1039	519	529	0	325	3486	58.1
		16.8	14.0		29.8	14.9	15.2		9.3		
3349	9	168	105	263	0	0	0	273	0	809	89.9
		20.8	13.0	32.5				33.7			
3627	70	1054	1324	2066	0	0	946	1142	0	6532	93.3
		16.1	20.3	31.6			14.5	17.5			
3734	14	158	132	0	281	140	143	0	88	942	67.3
		16.8	14.0		29.8	14.9	15.2		9.3		
4141	25	665	415	1529	0	0	0	535	0	3144	125.8
		21.2	13.2	48.6				17.0			
Total	320	4614	3926	6557	2134	1067	2034	4762	667	25761	80.5
		17.9	15.2	25.5	8.3	4.1	7.9	18.5	2.6		

sampled both before and after logging, including two valleys, seven lower slopes, seven upper slopes, and four hilltops for a total of 20 plots for each time period. In most cases, the pre-logging plots were re-located and re-sampled following logging using 1:1000 scale topographic maps and a single corner marker for each plot. In a few cases, however, logging did not occur in the pre-logging sample plot because the logging was carried out by a private contractor with no obligation to ensure that the pre-logging plots were actually logged. In those few cases, the post-logging plots were placed as close as possible to the pre-logging plots, within the same slope position type, and within the area affected by logging. Although unavoidable when the field treatment is not controlled by the researcher, this is a less than ideal condition as the microsite may change over a short distance even within one particular slope position location. Thus, rather than using paired sample comparisons, data analysis was based on grouped sample comparisons.

Sample quadrats for both strata were located within 20 x 20 m plots using a design that (1) systematically sampled each side of the plot and the centre portion of the plot and (2) matched the sampling design of past studies in the region so that future analyses could be conducted using the pooled data from numerous sites sampled during past years. Understory plant species (< 0.5 m high) and abundance (% cover) were sampled using 15 1×1 m quadrats systematically placed every four metres along each side of the plot and down the centre line of the plot in parallel fashion. Plant species and their abundance (% cover) in the sapling stratum (> 0.5 m high and < 10 cm diameter at breast height) were sampled in five 2.5×2.5 m quadrats located in each corner of the plot and in the centre of the plot. Samples were placed at least 40 m from the logging roads.

Only the common plant taxa (at least 50% frequency at either sampling time) were compared statistically for differences in mean abundance (Mann-Whitney U statistic) (Analytical Software 1994) between pre and post-logging conditions. The less common species were also compared but only qualitatively. Plant species richness was measured as the mean number of taxa per quadrat or per plot. Because few sapling species were found in each quadrat, species richness data were expressed and analysed only by plot and not by quadrat, and because there were so few plots for each slope position, only the combination of all slope positions was used for the comparative analysis of species richness for the sapling layer.

Ordinations derived from principal components analysis (PCA) (Analytical Software 1994) of the taxa with more than 50% frequency for both the understory and sapling strata (a total of 28 psuedospecies) were used to quantify the change in plant community composition attributable to logging (Manly 1986; Halpern 1988). PCA was chosen because of the homogeneity of the data set; all samples were collected in one stand of relatively uniform composition (Gauch 1982; Ter Braak & Prentice 1988). The change in plant community composition due to logging was quantified by calculating a community similarity index (CSI) from the ordinations. This index was derived by expressing the ratio of PCA ordination space shared by both the pre and post-logging communities relative to the total non-overlapping PCA ordination space occupied by the two communities as a percentage. For example, a CSI of 90% indicates a very high degree of similarity between the two plant communities being compared, whereas a CSI of 10% indicates a very low degree of similarity between the two plant communities. Plant taxonomy was based on Chambers *et al.* (1996).

Results

In total, 68 plant taxa were found in the understory stratum in the Owain Lake Stand, including 14 non-flowering plant taxa, 19 flowering herb taxa, six creeping shrub taxa, 20 tall shrub taxa, and nine tree taxa (Table 2). Of the total 68 plant taxa, 58 were observed during the pre-logging sampling and 54 were observed during the post-logging sampling. None of the taxa absent in the post-logging understory samples were present in the post-logging sapling stratum. The most significant decline in the number of taxa occurred within the non-flowering group, where prior to logging, 100% of the 14 taxa were observed and following logging, only 50% of the taxa were observed (Table 2). Those missing taxa included horsetails, interrupted club-moss, interrupted fern, lady fern, marginal wood fern, northern beech-fern, and wolf's claw club-moss.

A total of 34 plant taxa were found in the sapling stratum of the Owain Lake Stand, including four non-flowering plant taxa, six flowering herb taxa, 14 tall shrub taxa and ten tree taxa (Table 3). Of these 34 taxa, 29 were observed prior to logging and only 21 were observed following logging. Two taxa in the sapling stratum that were present prior to logging but not present following logging, and that were absent from the understory stratum at both sampling times, were red osier dogwood and yellow birch.

Three flowering herbs (Bicknell's cranesbill, black fringed bindweed, and pink lady's slipper), one creeping shrub (trailing arbutus), and six tall shrubs (American mountain ash, green alder, mountain holly, pin cherry, sheep laurel, and wild red raspberry) were missing from the pristine samples (Table 4). Those taxa missing from the logged samples included six non-flowering plants (horsetail, interrupted club moss, lady fern, marginal wood fern, northern beech fern, and wolf's claw club moss), three flowering herbs (false Solomon's seal, Indian cucumber root, one-sided wintergreen), two creeping shrubs (creeping snowberry, dwarf raspberry), three tall shrubs (prince's pine, showy mountain ash, and red osier dogwood), and one tree (yellow birch) (Table 4).

Shelterwood logging in the Owain Lake Stand also resulted in changes to species richness, vegetation biomass, and individual species abundance in both the understory and sapling strata. For understory species richness, valleys declined by 18% ($p = 0.05$), and both lower and upper slopes

Table 2 Understory plant taxa by relative frequency (no. of quadrat occurrences/300 × 100) and biomass (mean % cover) before and after shelterwood logging in the Owain Lake old-growth pine stand.

	Pre-logging		*Post-logging*	
Species by plant group	*Frequency*	*Biomass*	*Frequency*	*Biomass*
Non-flowering plants				
Bracken fern (*Pteridium aquilinum*)	85	2.80	95	6.40
Common polypody (*Polypodium virginianum*)	15	0.02	5	0.01
Evergreen wood fern (*Dryopteris spinulosa* var. *intermedia*)	25	0.25	50	0.28
Ground pine (*Lycopodium dendroideum*)	35	0.12	5	0.01
Horsetail (*Equisetum* spp.)	5	0.01	0	0.00
Interrupted club-moss (*Lycopodium anotinum*)	5	0.01	0	0.00
Interrupted fern (*Osmunda claytoniana*)	10	0.05	0	0.00
Lady fern (*Athyrium filix-femina* ssp. *angustum*)	5	0.01	0	0.00
Lichen	100	1.30	100	0.69
Marginal wood fern (*Dryopteris marginalis*)	5	0.02	0	0.00
Mosses and liverworts (*Bryophyta* spp.)	100	5.30	100	1.90
Northern beech-fern (*Phegopteris connectilis*)	5	0.01	0	0.00
Shining club-moss (*Huperzia lucidula*)	5	0.01	5	0.01
Wolf's claw club-moss (*Lycopodium clavatum*)	5	0.01	0	0.00
Flowering herbs				
Bicknell's cranesbill (*Geranium bicknellii*)	0	0.00	20	0.06
Black fringed bindweed (*Polygonum cilinode*)	0	0.00	15	0.01
Blue-bead lily (*Clintonia borealis*)	85	1.70	85	1.10
Bunchberry (*Cornus canadensis*)	85	0.72	95	0.97
Canada mayflower (*Maianthemum canadense*)	100	5.30	100	3.00
Cow wheat (*Melampyrum lineare*)	5	0.01	5	0.02
False Solomon's seal (*Maianthemum racemosum*)	15	0.02	0	0.00
Goldthread (*Coptis trifolia*)	35	0.10	30	0.21
Grasses (*Poaceae* spp.)	30	0.03	40	0.18
Indian cucumber root (*Medeola virginiana*)	15	0.08	0	0.00
Large-leaved aster (*Aster macrophyllus*)	95	4.30	100	3.00
Naked miterwort (*Mitella nuda*)	5	0.01	5	0.01
One-sided wintergreen (*Orthilia secunda*)	5	0.01	0	0.00
Pink lady's-slipper (*Cypripedium acaule*)	0	0.00	25	0.02
Rose-twisted stalk (*Streptopus roseus*)	30	0.08	20	0.11
Spreading dogbane (*Apocynum androsaemi-folium*)	25	0.11	20	0.13
Starflower (*Trientalis borealis*)	100	0.46	95	0.32
Violets (*Viola* spp.)	20	0.45	10	0.03
Wild sarsparilla (*Aralia nudicaulis*)	100	3.20	100	2.70
Creeping shrubs				
Creeping snowberry (*Gaultheria hispidula*)	5	0.01	0	0.00
Dwarf raspberry (*Rubus pubescens*)	5	0.01	0	0.00
Partridgeberry (*Mitchella repens*)	5	0.01	5	0.10
Trailing arbutus (*Epigaea repens*)	0	0.00	5	0.01
Twinflower (*Linnaea borealis*)	15	0.03	30	0.04
Wintergreen (*Gaultheria procumbens*)	50	0.10	45	0.13
Tall shrubs				
American mountain ash (*Sorbus americana*)	0	0.00	10	0.03
Beaked hazel (*Corylus cornuta*)	70	0.31	65	0.66
Bush honeysuckle (*Diervilla lonicera*)	95	2.40	100	3.20
Fly honeysuckle (*Lonicera canadensis*)	45	0.12	10	0.02
Green alder (*Alnus viridis* ssp. *crispa*)	0	0.00	20	0.12
Low sweet blueberry (*Vaccinium angustifolium*)	95	0.85	95	1.00
Mountain-holly (*Nemopanthus mucronatus*)	0	0.00	10	0.10
Mountain maple (*Acer spicatum*)	20	0.05	5	0.01
Northern wild raisin (*Viburnum cassinoides*)	20	0.06	20	0.22
Pin cherry (*Prunus pensylvanica*)	0	0.00	15	0.03
Prince's pine (*Chimaphila umbellata* ssp. *cisatlantica*)	5	0.01	0	0.00

Serviceberry (*Amelanchier* spp.)	25	0.04	15	0.04
Sheep laurel (*Kalmia angustifolia*)	0	0.00	10	0.02
Showy mountain ash (*Sorbus decora*)	5	0.01	0	0.00
Skunk currant (*Ribes glandulosum*)	5	0.01	10	0.02
Speckled alder (*Alnus incana* ssp. *rugosa*)	10	0.02	5	0.01
Striped maple (*Acer pensylvanicum*)	5	0.01	5	0.07
Velvet-leaf blueberry (*Vaccinium myrtilloides*)	40	0.20	60	0.24
Wild red raspberry (*Rubus idaeus* ssp. *melanolasius*)	0	0.00	25	0.04
Willow (*Salix* spp.)	5	0.01	10	0.07
Trees				
Balsam fir (*Abies balsamea*)	55	0.22	40	0.26
Black spruce (*Picea mariana*)	75	0.30	55	0.49
Eastern white cedar (*Thuja occidentalis*)	10	0.01	5	0.02
Eastern white pine (*Pinus strobus*)	90	0.15	80	0.25
Poplar (*Populus* spp.)	10	0.01	30	0.69
Red maple (*Acer rubrum*)	85	0.76	100	3.70
Red pine (*Pinus resinosa*)	5	0.01	5	0.01
White birch (*Betula papyrifera*)	20	0.03	55	0.27
White spruce (*Picea glauca*)	15	0.02	5	0.03

declined by 10% ($p = 0.04$ and 0.01 respectively) (Table 5). Of the four slope positions, only lower slopes showed a significant change in understory vegetation biomass, declining by 17% ($p = 0.03$) (Table 5). For the other slope positions, the understory vegetation biomass increased but at insignificant probability levels. A total of six individual understory taxa showed significant changes in abundance. Bracken fern, red maple, and white birch increased in abundance by 110% ($p = 0.04$), 363% ($p < 0.01$) and 800% ($p = 0.02$), respectively, whereas the moss and liverwort group, Canada mayflower and starflower declined by 110% ($p = 0.04$), 49% ($p = 0.02$), and 28% ($p = 0.03$), respectively (Table 5).

In general, the changes that followed shelterwood logging in the Owain Lake Stand were most intensive in the sapling stratum. For example, species richness for all slope positions combined decreased by 41% ($p < 0.01$) (Table 5). Except for hilltops, sapling layer vegetation biomass decreased significantly on all individual slope positions, including the combination of all slope positions (Table 5). Biomass on upper and lower slopes decreased by 76% ($p < 0.01$), biomass in valleys decreased by 49% ($p < 0.05$, and biomass on all slope positions taken together declined by 69% ($p < 0.01$) (Table 5). Five individual taxa declined in abundance, including beaked hazel by 92% ($p < 0.01$), balsam fir and white spruce each by 86% ($p = 0.02$ and $p = 0.01$, respectively), white birch by 85% ($p = 0.04$) and bush honeysuckle by 58% ($p = 0.04$) (Table 5).

These changes in species richness, vegetation biomass, and abundance of individual plant taxa have resulted in a major shift in plant community composition in the Owain Lake Stand. The pristine understory community was dominated primarily by herbaceous flowering plants, including Canada mayflower (5.3%), large-leaved aster (4.3%), wild sarsparilla (3.2%) and blue-bead lily (1.7%) with a significant component of the moss and liverwort group (5.4%) and lichens (1.4%) (Table 6). Following logging, the understory plant community shifted to one dominated by bracken fern (6.4%) and woody plants, including red maple (3.7%) and bush honeysuckle (3.2%) (Table 6). Prior to logging, the sapling stratum was dominated by trees, including balsam fir (8.1%) and red maple (7.5%), bracken fern (7.5%), and the shrub, beaked hazel (6.1%) (Table 6). With four months of growth, the sapling stratum had shifted to a community dominated primarily by bracken fern (5.7%) and red maple (2.6%) (Table 6), both of which were also the two most dominant taxa in the understory following logging.

The first two axes of the PCA together explained 48% of the variation within all 40 sample plots (PCA axis 1 = 28.7% and axis 2 = 19.0%). The CSI that was used to quantify the change in composition between pre and post-logging plant communities in the Owain Stand was highest for all slope positions taken together (8.3%) and declined progressively from hilltops (7.4%) to lower slopes (3.9%) and finally to upper slopes (0%) and valleys (0%) (Figs. 1–5). In other words, the effect of shelterwood logging was greatest on valley and upper slope plant communities (Figs. 4–5) and least on lower slope and hilltop communities (Figs. 2–3). On all slope positions, logging shifted the composition of the plant community towards the positive end of PCA axis 1 which was typified by species commonly associated with drier open–canopy conditions such as bracken fern, whereas the negative end of PCA axis 1, where the pristine samples are clustered, was characterized by taxa such as bryophytes, which are more typical of moist-closed canopy conditions. In addition, the ordination space of the logged communities was in all cases much smaller than the ordination space of the pristine communities (Figs. 2–5), indicating a more constricted group of common plant species in the logged community.

Essentially, the understory plant community shifted from one dominated by mosses and liverworts (5.4% cover), Canada mayflower (5.3% cover), and large-leaved aster (4.3% cover) to a community dominated by bracken fern

Table 3 Sapling layer plant taxa by relative frequency (no. of quadrat occurrences/100 × 100) and biomass (mean % cover) before and after shelterwood logging in the Owain Lake old-growth pine stand.

Species by plant group	*Pre-logging*		*Post-logging*	
	Frequency	*Biomass*	*Frequency*	*Biomass*
Non-flowering plants				
Bracken fern (*Pteridium aquilinum*)	85	8.10	95	5.70
Evergreen wood fern (*Dryopteris spinulosa* var. *intermedia*)	15	0.82	0	0.00
Interrupted fern (*Osmunda claytoniana*)	15	0.82	0	0.00
Lady fern (*Athyrium filix-femina* ssp. *angustum*)	5	0.01	0	0.00
Flowering herbs				
False Solomon's seal (*Maianthemum racemosum*)	5	0.01	0	0.00
Indian cucumber root (*Medeola virginiana*)	15	0.08	0	0.00
Large-leaved aster (*Aster macrophyllus*)	0	0.00	10	0.02
Rose-twisted stalk (*Streptopus roseus*)	0	0.00	5	0.01
Spreading dogbane (*Apocynum androsaemifolium*)	15	0.06	15	0.03
Wild sarsparilla (*Aralia nudicaulis*)	10	0.05	5	0.05
Tall shrubs				
American mountain ash (*Sorbus americana*)	0	0.00	10	0.06
Beaked hazel (*Corylus cornuta*)	85	6.10	35	0.50
Bush honeysuckle (*Diervilla lonicera*)	70	0.64	35	0.31
Fly honeysuckle (*Lonicera canadensis*)	10	0.31	0	0.00
Green alder (*Alnus viridis* ssp. *crispa*)	0	0.00	5	0.05
Mountain-holly (*Nemopanthus mucronatus*)	0	0.00	5	0.10
Mountain maple (*Acer spicatum*)	25	0.82	0	0.00
Northern wild raisin (*Viburnum cassinoides*)	30	0.24	5	0.05
Red osier dogwood (*Cornus stolonifera*)	5	0.03	0	0.00
Serviceberry (*Amelanchier* spp.)	15	0.03	0	0.00
Showy mountain ash (*Sorbus decora*)	10	0.06	0	0.00
Speckled alder (*Alnus incana* ssp. *rugosa*)	15	0.73	5	0.20
Velvet-leaf blueberry (*Vaccinium myrtilloides*)	20	0.10	5	0.10
Willow (*Salix* spp.)	25	0.07	15	0.09
Trees				
Balsam fir (*Abies balsamea*)	85	8.10	60	1.10
Black spruce (*Picea mariana*)	55	3.40	50	1.00
Eastern white cedar (*Thuja occidentalis*)	20	0.17	0	0.00
Eastern white pine (*Pinus strobus*)	30	0.10	10	0.08
Poplar (*Populus* spp.)	25	0.18	30	0.67
Red maple (*Acer rubrum*)	85	7.60	75	2.60
Red pine (*Pinus resinosa*)	10	0.07	0	0.00
White birch (*Betula papyrifera*)	55	2.00	20	0.31
White spruce (*Picea glauca*)	65	2.80	30	0.40
Yellow birch (*Betula alleghaniensis*)	5	0.03	0	0.00

(6.4% cover), red maple (3.7% cover) and bush honeysuckle (3.2% cover) (Table 6). In the sapling layer, the top three taxa in the pristine condition remained as the top three taxa following logging. Their order of abundance changed, however, and their total biomass was severely reduced. These top three taxa, from most to least abundant prior to logging, were balsam fir (8.1% cover), red maple (7.5% cover) and bracken fern (7.5% cover). All three declined in abundance following logging with bracken fern (5.7% cover) becoming most abundant, balsam fir (1.1% cover) becoming least abundant, and red maple maintaining its intermediate ranking at 2.6% cover (Table 6).

Discussion

Numerous changes occurred within the understory and sapling vegetation in the Owain Lake Stand within the first four months of the growing season following shelterwood logging. These changes included declines in species richness, declines in vegetation biomass, declines and increases in both uncommon and common plant taxa, and major shifts in plant community composition for all habitat conditions. Although changes in habitat conditions at the forest floor were observed (e.g. more light and drier upper soil conditions), they were only qualitatively assessed. However, changes from a humid,

Table 4 Understory and sapling plant taxa that were absent from either the pristine or the logged sites (* = early successional invasive species).

Absent in the pristine condition	*Absent in the logged condition*
Non-flowering plants	
(none)	Horsetail
	Interrupted club moss
	Lady fern
	Marginal wood fern
	Northern beech fern
	Wolf's claw club moss
Flowering herbs	
Bicknell's cranesbill *	False Solomon's seal
Black fringed bindweed *	Indian cucumber root
Pink lady's-slipper	One-sided wintergreen
Creeping shrubs	
Trailing arbutus	Creeping snowberry
	Dwarf raspberry
Tall shrubs	
American mountain ash	Prince's pine
Green alder	Showy mountain ash
Mountain holly	Red osier dogwood
Pin cherry *	
Sheep laurel	
Wild red raspberry *	
Trees	
(none)	Yellow birch

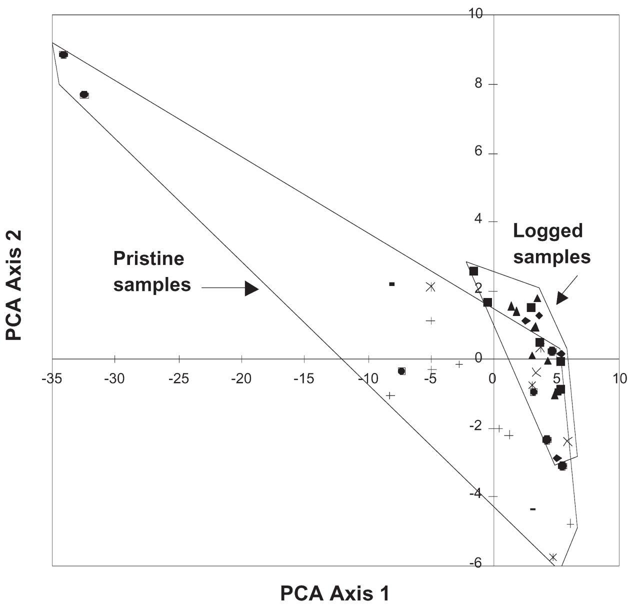

Figure 1 PCA ordination of all slope positions for the pristine and logged plant communities in the Owain Lake Stand (CSI = 8.3%). Key to symbols: ◆ = logged hilltop; ■ = logged lower slope; ▲ = logged upper slope; × = logged valley; ✻ = pristine hilltop; ● = pristine lower slope; + = pristine upper slope; − = pristine valley.

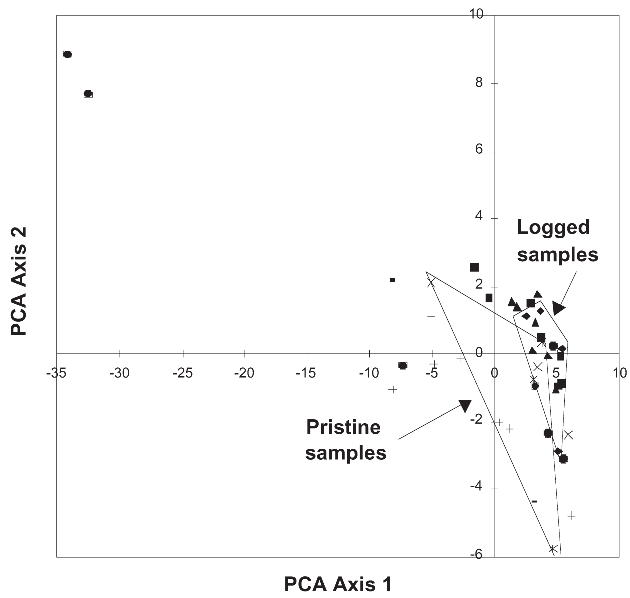

Figure 2 PCA ordination of hilltops for the pristine and logged plant communities in the Owain Lake Stand (CSI = 7.4%). For symbols, see Figure 1 legend.

Table 5 Species richness, biomass, and composition in the understory and sapling strata of the Owain Lake old-growth pine stand following shelterwood logging (n = number of samples for each of the pristine and logged conditions; p = plots, q = quadrats; % change is calculated relative to the pristine condition).

Vegetation feature and location	*n*	*Mean pristine*	*Mean logged*	*Probability value*	*Change (%)*
Understory (0–0.5 m)					
Species richness					
All slope positions	20 p	20.90	20.80	0.7972	
Valleys	30 q	7.80	6.40	0.0565	−18
Lower slopes	105 q	6.90	6.20	0.0378	−10
Upper slopes	105 q	7.10	6.40	0.0087	−10
Hilltops	60 q	6.70	6.20	0.1273	−7
Biomass (% cover)					
All slope positions	20 p	32.10	33.10	0.9569	+3
Valleys	30 q	32.80	40.80	0.1224	+24
Lower slopes	105 q	32.80	27.30	0.0297	−17
Upper slopes	105 q	31.10	33.40	0.8970	+7
Hilltops	60 q	31.30	36.10	0.1777	+15
Composition (% cover)					
Lichens	20 p	1.40	0.70	0.1850	−50
Mosses and liverworts	20 p	5.40	2.00	0.0045	−63
Bracken fern	20 p	3.10	6.50	0.0425	+110
Wood fern	20 p	0.27	0.29	0.2184	+7
Blue-bead lily	20 p	1.70	1.10	0.5338	−35
Bunchberry	20 p	0.72	0.99	0.4652	+38
Canada mayflower	20 p	5.30	2.70	0.0231	−49
Large-leaf aster	20 p	4.30	3.00	0.3104	−30
Starflower	20 p	0.46	0.33	0.0256	−28
Wild sarsparilla	20 p	3.20	2.70	0.8077	−16
Beaked hazel	20 p	0.31	0.66	0.5075	+113
Late-low blueberry	20 p	0.90	1.00	0.3235	+11
Bush honeysuckle	20 p	2.40	3.20	0.3867	+33
Velvet-leaved blueberry	20 p	0.20	0.24	0.6073	+20
Wintergreen	20 p	0.10	0.13	0.8498	+30
Balsam fir	20 p	0.22	0.26	0.7150	+18
Black spruce	20 p	0.30	0.49	0.6263	+63
Red maple	20 p	0.80	3.70	0.0017	+363
White birch	20 p	0.03	0.27	0.0207	+800
White pine	20 p	0.15	0.25	0.2036	+64
Sapling stratum (0.5 m–10 cm dbh)					
Species richness					
All slope positions	20 p	9.00	5.30	0.0002	−69
Biomass (% cover)					
All slope positions	20 p	46.60	13.40	0.0000	−69
Valleys	10 q	47.90	24.30	0.0452	−49
Lower slopes	35 q	42.00	9.90	0.0000	−76
Upper slopes	35 q	46.70	11.30	0.0000	−76
Hilltops	20 q	30.70	17.40	0.1017	−43
Composition (% cover)					
Bracken fern	20 p	7.50	5.70	0.2793	−24
Beaked hazel	20 p	6.10	0.50	0.0006	−92
Bush honeysuckle	20 p	0.64	0.27	0.0439	−58
Balsam fir	20 p	8.10	1.10	0.0200	−86
Black spruce	20 p	3.40	1.00	0.3169	−71
Red maple	20 p	7.50	2.60	0.0787	−65
White birch	20 p	2.00	0.30	0.0439	−85
White spruce	20 p	2.80	0.40	0.0119	−86

Table 6 Mean biomass (% cover) of the most common understory and sapling layer taxa before and after shelterwood logging in the Owain Lake old-growth pine stand (mean % cover ⩾ 1.0; * = % cover means differed significantly between conditions).

Pristine condition		*Logged condition*	
Species	*Biomass*	*Species*	*Biomass*
Understory			
Moss and liverwort	5.4*	Bracken fern	6.4*
Canada mayflower	5.3*	Red maple	3.7*
Large-leaved aster	4.3	Bush honeysuckle	3.2
Wild sarsparilla	3.2	Large-leaved aster	3.0
Bracken fern	2.8*	Canada mayflower	3.0*
Bush honeysuckle	2.4	Wild sarsparilla	2.7
Blue-bead lily	1.7	Blue-bead lily	1.1
Lichen	1.4	Sweet low blueberry	1.0
Sapling layer			
Balsam fir	8.1*	Bracken fern	5.7
Red maple	7.5	Red maple	2.6
Bracken fern	7.5	Balsam fir	1.1*
Beaked hazel	6.1*	Black spruce	1.0
Black spruce	3.4		
White spruce	2.8*		
White birch	2.0*		

shady microclimate to a dry, light-intensive environment at the forest floor due to logging resulting in the severe reduction of mosses, liverworts, and lichens have been documented by many studies (e.g. Soderstrom 1988; Lesica *et al.* 1991; Laaka 1992). It is unlikely that all the changes observed in this study will be permanent, however it is likely that those changes involving species with vigorous growth and prolific reproduction will have a significant influence on the future forest community.

Overall, there were six fewer plant taxa observed in the logged quadrats compared to those observed in the pristine quadrats in the Owain Stand. Selection logging, the least

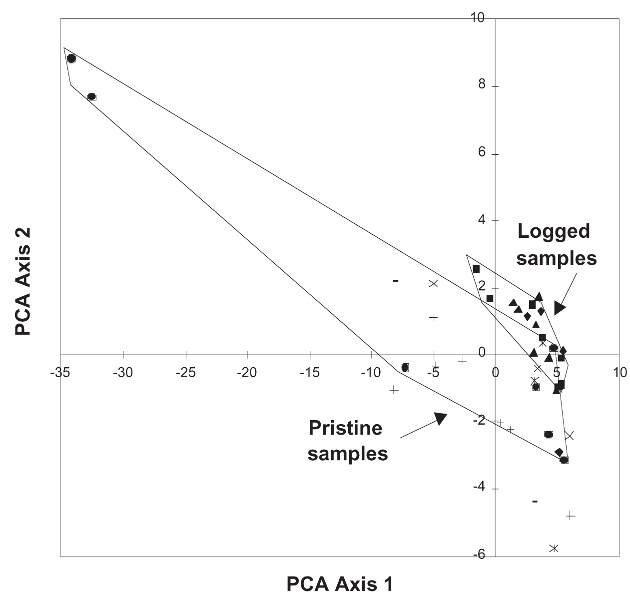

Figure 3 PCA ordination of lower slopes for the pristine and logged plant communities in the Owain Lake Stand (CSI = 3.9%). For symbols, see Figure 1 legend.

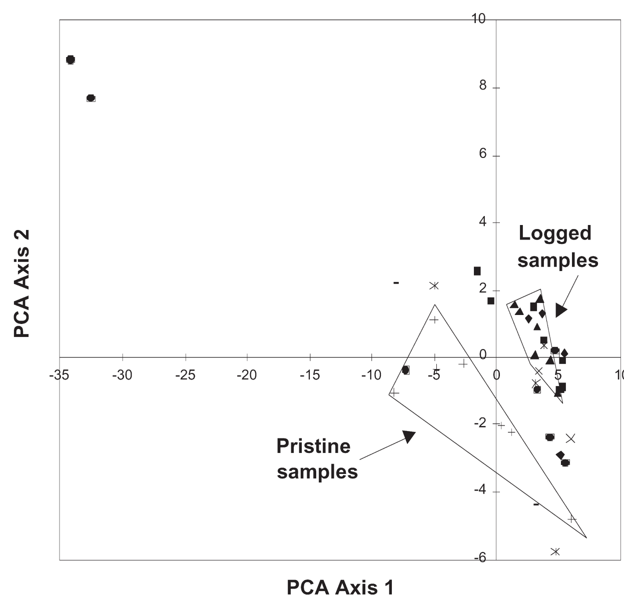

Figure 4 PCA ordination of upper slopes for the pristine and logged plant communities in the Owain Lake Stand (CSI = 0%). For symbols, see Figure 1 legend.

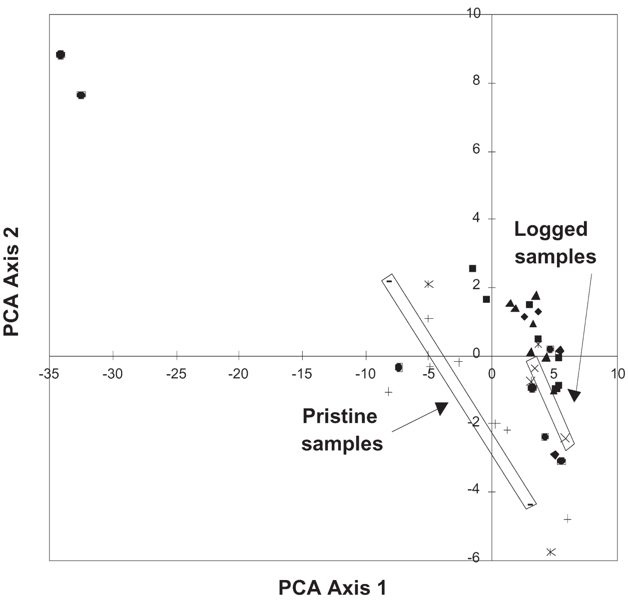

Figure 5 PCA ordination of valleys for the pristine and logged plant communities in the Owain Lake Stand (CSI = 0%). For symbols, see Figure 1 legend.

intrusive of logging practices, has also resulted in the loss of species from study plots in mature deciduous forests (Metzger & Schultz 1984; Reader 1987). In a mature white pine/red pine/mixed forest in central Ontario, Sidhu (1973) found that some understory plant species present in the control area (unlogged) were absent from samples in the area that was shelterwood logged. At a more intensive level than shelterwood logging, North *et al.* (1996) found that both a green tree retention cut (seed tree) and a clearcut in a western hemlock-dominated stand lacked five understory taxa (one fern, two herbs and two trees) that were present in the uncut mature forest serving as the control. In addition, clearcut logging in old-growth Douglas fir forests of Oregon resulted in up to a 29% loss of the original understory taxa one growing season after logging (Halpern & Spies 1995). A mean of about five species extinctions from their study areas was documented by both Dyrness (1973) and Halpern & Spies (1995).

Four of the taxa in the Owain Lake Stand that were present in the logged samples but not in the pristine samples were early successional invasive species, including Bicknell's cranesbill, black fringed bindweed, pin cherry, and wild red raspberry, all of which are commonly found in recently cut areas (Chambers *et al.* 1996). Colonization by invasive plant species following logging has also been observed in the hardwood forests of New England (Bormann & Likens 1979), Wisconsin (Rogers 1959), Michigan (Metzger & Schultz 1984), the mid-western USA (Outcalt & White 1981), the conifer forests of the south-eastern USA (McComb & Noble 1982) and the Pacific North-western USA (Dyrness 1973; Corns & LaRoi 1976; Halpern & Spies 1995). Thus, excluding the four invasive species, only six non-invasive understory taxa found in the logged areas were not included in the samples of the pristine condition, whereas 15 taxa found in the pristine pine forest were missing from the logged samples. All but two of these taxa (each with 15% frequency) that were not included in the logged samples had a frequency of only 5% (found in only one of 20 plots) in the pristine condition. This rarity combined with the shady, moist conditions required for most non-flowering plants, most likely renders them vulnerable to the physical disturbance of logging and the resulting increase in light intensity and decreased moisture at the forest floor (MacLean & Wein 1977: Metzger & Schultz 1984; Meier *et al.* 1995).

Species richness in the Owain Lake Stand was most severely reduced in the sapling layer (69%). In the understory, species richness was reduced most severely in the valleys (18%) but was also significantly reduced on upper and lower slopes (10% each). Elsewhere, species richness of the herbaceous plant community was reduced by an average of 39% following clearcutting in nine different mixed-mesophytic forest stands throughout the south-eastern USA with no trend in species richness recovery over time (Duffy & Meier 1992). Strip cutting of northern hardwood forests resulted in higher levels of plant species richness compared with block clearcutting, which after ten years of recovery showed a decreasing trend in species richness (Gove *et al.* 1992). In old-growth Douglas-fir forests of the Pacific North-western USA, the old-growth stage has the highest level of plant diversity whereas recent clearcuts had the lowest levels (Long 1977; Halpern & Spies 1995). In sugar maple-dominated forests of Michigan, selection cuts, partial cuts and clearcuts all resulted in the reduction of species richness (Metzger & Schultz 1984). Even thinning of hardwood cove forests in North Carolina resulted in a 16% decrease in species richness of vernal herbs, and clearcutting increased losses to 28% (Meier *et al.* 1995).

Vegetation biomass reduction in the Owain Lake Stand was also most severe in the sapling layer (ranging from 49% to 76%), occurring on all slope positions except hilltops which showed a reduction of 43% but at an insignificant probability level (0.10). The only significant change in understory vegetation biomass of the Owain Lake Stand was a reduction (17%) on the lower slopes. Shelterwood logging in larch/Douglas-fir forests also resulted in a significant reduction in understory vegetation biomass four years after harvest (Schmidt 1980), and clearcutting in nine different mixed-mesophytic forests in the south-eastern USA resulted in an average decrease of 60% in understory herbaceous biomass (Duffy & Meier 1992) with no evidence indicating a trend towards recovery of pre-logging conditions.

The five sapling layer taxa in the Owain Lake Stand that changed significantly following shelterwood logging all decreased in abundance ranging from a 58% to a 92% decrease, including beaked hazel, bush honeysuckle, balsam fir, white birch and white spruce. Sidhu (1973) also found that shelterwood logging in a white pine/red pine/mixed-woods stand decreased beaked hazel by 64% and balsam fir by 60% in the sapling stratum. In the understory of the Owain Lake Stand, three taxa decreased significantly, ranging from a 28% to a 63% decrease, including mosses and liverworts, Canada mayflower and starflower. In contrast, three understory species increased significantly, ranging from a 110% to an 800% increase, including bracken fern, red maple and white birch. Sidhu (1973) also found that the relative abundance (biomass) of many understory plant species changed following shelterwood logging and four months of post-logging growth, including a decrease in starflower and an increase in bracken fern, red maple and white birch.

After four months of growing season following shelterwood logging, the understory of the Owain Lake Stand shifted from a community primarily dominated by herbaceous plants (Canada mayflower, large-leaved aster, wild sarsparilla, and blue-bead lily) and non-flowering plants (mosses and liverworts, and lichens) to a community with a greater content of woody plants (red maple, bush honeysuckle and sweet low blueberry) and bracken fern. Both Long (1977) and Metzger and Schultz (1984) also found an increase in woody plants in the forest understory following logging. Increases in the abundance of red maple following logging in Wisconsin and Michigan have also been documented by Nowacki *et al*. (1990) and Palik and Pregitzer (1992). Herb and moss species may recover as the canopy closes and the shrub layer declines as observed for a successional sequence in Douglas-fir forest (Long 1977). However, since the remaining overstory of the Owain Lake shelterwood cut is scheduled to be removed in 20 to 40 years in order to complete the logging operation, it is likely to be a century or more before its canopy approaches closure.

In addition, red maple, bracken fern and bush honeysuckle, which are the three most important species in the post-logging understory plant community, will most likely increase in abundance under the present disturbed condition. It is also likely that their growth and spread will be further facilitated when the second shelterwood cut occurs removing most of the remaining overstory tree biomass. All three species are vigorous vegetative reproducers, either sprouting from the base of the stem or from rhizomes. Red maple is also extremely competitive due to its moderate shade tolerance, its relatively fast growth rate, its regular and abundant seed crop production, and its minimal seedbed requirements (Bently & Pinto 1994). As a result of logging, fire suppression, and other human disturbances, red maple has increased from a pre-settlement abundance ranging from one to 12% in many portions of eastern North America to become one of the most abundant and widespread tree species in that region (Abrams 1999). In fact, according to Abrams (1999), the present rapid increase in the abundance of red maple throughout the forests of eastern North America will be one of the primary causes for the decline of oak and pine-dominated forests. Bracken fern also grows very rapidly (Conway 1952). For example one rhizome from a single colony can grow as much as 21 m in one season. In addition, it can suppress herbaceous plants and tree seedlings through shading and by producing allelopathic chemicals that prohibit and reduce germination and growth of other plant species (Bently & Pinto 1994).

Given this increased competition from red maple, bracken fern and bush honeysuckle, and the lack of any increase in abundance for either red or eastern white pine, some kind of future management will probably be required to ensure that the stand is repopulated with pine. This might include a light to medium-intensity fire that would burn through the forest understory or mechanical site preparation just prior to a productive pine seed year to reduce competition. As a last resort, planting of red and eastern white pine seedlings may also be required. Future studies should focus on the longer-term effects of shelterwood logging on forest composition and diversity, and on identifying the level of overstory biomass removal that minimizes forest community changes and maximizes successful pine regeneration.

Conclusion

Relative to the pristine condition, ten fewer taxa were found following logging. Of all plant groups, the most significant decline in the number of taxa following logging was in the understory non-flowering group (50% decrease). Logging reduced species richness most severely in the sapling stratum, but significant reductions in understory species richness also occurred in valleys, on lower slopes, and on upper slopes. Significant changes in total vegetation biomass were restricted to reductions only and were most severe in the sapling stratum on each slope position except for hilltops. Understory vegetation biomass was significantly reduced on lower slopes only. Significant increases and decreases in the abundance of individual plant taxa were found in the understory stratum, whereas in the sapling stratum, only significant decreases in the abundance of individual plant taxa were found. In the understory, increases included white birch by 800%, red maple by 363% and bracken fern by 110%; decreases included mosses and liverworts by 110%, Canada mayflower by 49% and starflower by 28%. In the sapling stratum, the decreases included beaked hazel by 92%, balsam fir and white spruce each by 86%, white birch by 85% and bush honeysuckle by 58%. Thus, the understory plant community shifted from one dominated by non-flowering plants and herbaceous plants to a community dominated by bracken fern and woody plants. Dominance in the sapling stratum was maintained by bracken fern and woody plants. Changes in plant community composition of the two strata combined were greatest in valleys and on upper slopes, least on hilltops, and at an intermediate level on lower slopes. Bracken fern, red maple and bush honeysuckle, the three most abundant species in the post-harvest understory plant community, will probably increase in their abundance under the present disturbed condition. A second shelterwood cut in 20 to 40 years may further facilitate an increase in these three species primarily by increasing light levels at the forest floor. All three species are very vigorous and will probably dominate the forest understory until the upper canopy closes. Since old-growth red and eastern white pine forests are a critically endangered forest ecosystem type (> 98% decline: Noss *et al*. 1995; Quinby 1993, 1996*a*), it is the position of many scientists, resource managers, and environmentalists that any further logging should be excluded from this forest type (Johnson 1998).

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