ELSEVIER

# The effects of partial harvest on the understory vegetation of southern Ontario woodlands

Dawn M. Burke [a,*], Ken A. Elliott [a], Stephen B. Holmes [b], David Bradley [c]

[a] Ontario Ministry of Natural Resources, Science and Information Branch, 659 Exeter Road, London, ON N6E 1L3, Canada
[b] Natural Resources Canada, Canadian Forest Service, 1219 Queen Street E., Sault Ste. Marie, ON P6A 2E5, Canada
[c] Ontario Ministry of Natural Resources, Southern Science and Information Branch, 300 Water Street, 4th Floor, South Tower, Peterborough, ON K9J 8M5, Canada

## Abstract

We studied the effects of partial cutting on understory vegetation communities within 19 mixed maple forests in an agriculture-dominated landscape in southwestern Ontario. Woodlots that had been recently harvested were grouped according to provincial silviculture guidelines (standard and heavy cuts) and compared to woodlots that had been uncut for at least 24 years (reference stands). We found significant differences in richness, diversity, and quality of understory vegetation in response to harvest indices. More intensive harvesting resulted in increased richness and diversity, but mostly through the addition of habitat generalists and weedy species. However, partial harvest does not appear to drive vegetation community composition, as ordination methods found no clear community differences between the treatments. Use of the single-tree selection system based on basal area and harvest intensity targets will have an effect on the understory plants, but other factors including past management, disturbance history, and site level microclimate features will also play an important role in shaping vegetation communities. We caution against the removal of large volumes of trees ≥38 cm in diameter, and large reductions in canopy cover, as this can reduce the presence of "conservative" (forest dependent specialist) species, despite a general increase in species richness and diversity. Furthermore, we recommend additional research to investigate the potential for incremental degradation to occur on sites with a long-term history of harvesting, as we found that richness of exotics increased on sites with a history of forest management.
© 2008 Elsevier B.V. All rights reserved.

Keywords: Hardwood forests; Herbaceous vegetation; Logging; Non-native plants; Plant-species diversity; Plant-species richness; Selection system

## 1. Introduction

Forest management is a widespread disturbance in forested ecosystems that may threaten the survival of species through the alteration of substrate availability and environmental conditions. The importance of devising silviculture systems that sustain biodiversity while still meeting the goals for timber production has prompted researchers to evaluate the impacts of forest management techniques on more than just traditional measures of success (i.e. regeneration, growth and yield of desirable species). The maintenance of plant species diversity in the understory should be an important goal of current silviculture prescriptions, not only because of their sensitivity to disturbance (but see Kern et al., 2006) but also because of the

essential role they play in ecosystem structure and function (MacLean and Wein, 1977; Roberts and Gillam, 1995). Given the general acceptance that logging should have a long-term neutral effect, there is growing concern that timber harvesting may negatively affect the long-term maintenance of species diversity and composition, particularly with increasing disturbance intensity.

Much of the native woodland vegetation in southern Ontario is now restricted to small, isolated, and often modified remnants of forest (Francis et al., 2000). Although the landscape is highly fragmented, and woodlots may be very small, logging is prevalent, and may compound losses to forest biodiversity. Most of the deciduous forests in this region are privately owned and are periodically partially cut for timber and fuelwood (Reader and Bricker, 1992). The structure and composition of the upland tolerant hardwood forests that once dominated the landscape in much of southern Ontario evolved under a history of abundant, small-scale disturbances that caused canopy gaps

ranging in size from a single tree to a small group of trees (Runkle, 1991). In these forests, the selection system tends to mimic small-scale disturbances and has been recommended as a way of maintaining forest biodiversity while still allowing for timber extraction (McComb et al., 1993; Annand and Thompson, 1997; Norton and Hannon, 1997; Steventon et al., 1998; Chambers et al., 1999; Robinson and Robinson, 1999; Schieck and Hobson, 2000; Simon et al., 2000). However, information relating past harvest practices to current understory and overstory conditions in managed forests is scarce (but see Halpern and Spies, 1995; Thysell and Carey, 2000). This information is needed in order to predict the effects of future anthropogenic disturbances on biodiversity, stand development, and long-term ecosystem structure and function.

Many studies on the consequences of forest management for plant species diversity and composition have been concerned with the success of regenerating tree species and stand structure. Fewer studies have addressed the response of plants, particularly understory vegetation, to logging or gap creation in deciduous forests (*natural gaps*: Ehrenfeld, 1980; Thompson, 1980; Moore and Vankat, 1986; *partial harvest*: Metzger and Schultz, 1981, 1984; Collins and Pickett, 1987; Reader, 1987; Reader and Bricker, 1992; Hammond and Brown, 1998; Fredericksen et al., 1999; Götmark et al., 2005 and *clear-cutting*: Metzger and Schultz, 1981, 1984; Duffy and Meier, 1992; Gilliam et al., 1995; Meier et al., 1995; Hammond and Brown, 1998; Fredericksen et al., 1999; Gilliam, 2002). However, species may be lost from the forest understory because of tree harvesting, skidding, and slash accumulation that occurs as a direct result of harvest operations, and/or because of the micro-environmental changes that occur in response to canopy removal (Reader, 1987; Reader and Bricker, 1992).

The effect of harvesting on the understory vegetation will have important consequences for vegetation composition, productivity, aesthetics, wildlife habitat, water and nutrient cycling (Metzger and Schultz, 1984). Current research suggests that intensive harvests (i.e. clear-cutting) will have a greater impact on understory species than partial harvest techniques, because the latter has less drastic effects on substrate availability and environmental conditions (Meier et al., 1995; Hammond and Brown, 1998; Jalonen and Vanha-Majamaa, 2001; Økland et al., 2003; Zenner et al., 2006). Several studies have shown that forest herbs are largely unaffected by partial canopy removal, particularly if given enough time for regrowth (Metzger and Schultz, 1984; Collins and Pickett, 1987; Reader and Bricker, 1992; Kern et al., 2006).

The purpose of this research was to study the impacts of partial harvest on the understory vegetation communities within mixed maple forests in an agriculture-dominated landscape in southwestern Ontario. We relate patterns of species richness, diversity, abundance, and composition within these sites to the intensity of partial harvest for recently harvested and reference tolerant hardwood stands. Specifically we address the following questions: (1) what is the response of the understory to forest management techniques; (2) how does this vary between life forms of ground flora; (3) how do plant communities differ between treatment types; and (4) does partial harvesting reduce the quality of the post-harvest vegetation and/or result in changes to the richness of invasives and/or habitat generalists?

## 2. Methods

### 2.1. Study sites

This study was conducted in 19 upland tolerant hardwood forest fragments scattered across the Carolinian Zone of southwestern Ontario, within 75 km of the city of London (Table 1). Within this region, the landscape is primarily agricultural and urban, with an average forest cover of 13% (Larson et al., 1999). Upland forests selected for study had to be dominated by one or both upland maple species (sugar maple *Acer saccharum* Marsh., red maple *Acer rubrum* L.) and also contain American beech (*Fagus grandifolia* Ehrh.) and white ash (*Fraxinus americana* L.) as additional main canopy species. Other common species associates found at varying levels on most sites included red oak (*Quercus rubra* L.), red (green) ash (*Fraxinus pennsylvannica* Marsh.), silver maple (*Acer saccharinum* L.), bitternut hickory (*Carya cordiformis* (Wangenh.)), black cherry (*Prunus serotina* Ehrh.), and basswood (*Tilia american* L.).

Woodlots within each treatment covered a similar range of woodland area (Table 1). In order to maximize comparability among stands, in additional to having similar species compositions in the overstory, study sites (1) had uniform forest management history over the entire area sampled, (2) lacked signs of additional severe natural disturbance (i.e. ice-storm, hurricane damage), (3) had similar topography, and (4) were medium to high quality sites that were mesic and moderately well drained with sandy to sandy-loam soils. Sites were predominantly classified as the Fresh to Moist Sugar Maple—Hardwood Deciduous Forest Ecosite Type (Lee et al., 1998).

Twelve woodlots were partially harvested at varying intensities between 1994 and 1999 (residual basal area (RBA) range: 14.2–26.5. $m^2$/ha). Seven woodlots had not been harvested for at least 24 years, and functioned as reference sites (basal area range: 27.3–37.2 $m^2$/ha). Harvested woodlots were grouped according to provincial silviculture guidelines for the selection system based on RBA stocking targets for maximizing sawlog production in Site Region 7E (Carolinian Zone) and % removal of basal area (Ontario Ministry of Natural Resources, 2000). Total RBAs were calculated for all trees $\geq$2.5 cm in diameter-at-breast-height (dbh). These were measured in treated blocks in 1999 (1–5 years after harvesting) and in control blocks in 2000 ($\geq$24 years after any commercial harvesting). We considered woodlots with total RBAs more than 1.5 $m^2$/ha below the provincial target of 20.5 $m^2$/ha to be *heavy cut* and those within or above the target to be *standard cut* (Table 1). We used diameters and heights of measured stumps to reconstruct pre-harvest basal areas for all harvested woodlots (Honer et al., 1983). Based on these values, we were able to determine how much basal area was removed during harvest.

Table 1
Woodlot characteristics for 19 woodlands sampled in Middlesex, Elgin, Oxford, Norfolk and Brant counties, in southwestern Ontario, Canada

| Woodlot ID | Woodland area (ha) | Harvest block area (ha) | Year cut | Pre-harvest BA[a] (m²/ha) | Residual BA[b] (m²/ha) | % BA harvested (%) |
|---|---|---|---|---|---|---|
| Reference[c] | | | | | | |
| 401 | 189.6 | 0 | 1968 | NA[d] | 30.9 | 0 |
| 402 | 106.3 | 0 | 1975–1976[e] | NA | 31.2 | 0 |
| 403 | 261.6 | 0 | U[f] | NA | 37.1 | 0 |
| 404 | 30.7 | 0 | U[f] | NA | 27.3 | 0 |
| 407 | 20.1 | 0 | U[f] | NA | 37.2 | 0 |
| 408 | 41.2 | 0 | U[f] | NA | 33.4 | 0 |
| 409 | 38.2 | 0 | U[f] | NA | 32.7 | 0 |
| Average | 98.2 | | | NA | 32.3 | 0 |
| S.D. | 93.6 | | | NA | 3.6 | NA |
| Standard[c] | | | | | | |
| 8 | 27.9 | 18.3 | 1998 | 25.8 | 23.1 | 10.4 |
| 19 | 56.7 | 56.6 | 1995 | 25.0 | 22.2 | 11.5 |
| 42 | 21.6 | 17.3 | 1998 | 27.0 | 23.0 | 14.7 |
| 78 | 139.9 | 28 | 1997 | 34.6 | 26.6 | 23.2 |
| 77 | 139.9 | 24.8 | 1995 | 33.1 | 25.6 | 22.6 |
| 105 | 92.2 | 12.1 | 1998 | 25.0 | 20.0 | 20.0 |
| 108 | 25 | 12.2 | 1999 | 22.5 | 20.5 | 8.9 |
| Average* | 71.9 | | | 27.6 | 23.0 | 15.4 |
| S.D. | 52.5 | | | 4.5 | 2.4 | 6.0 |
| Heavy[c] | | | | | | |
| 36 | 104.9 | 12.1 | 1998 | 24.4 | 15.1 | 38.3 |
| 86 | 14.9 | 10.6 | 1997 | 26.0 | 17.2 | 34.0 |
| 107 | 49.6 | 13 | 1997 | 21.6 | 14.2 | 34.3 |
| 121 | 25.9 | 15.3 | 1996 | 35.8 | 19.6 | 45.3 |
| 300 | 154.3 | 74 | 1998 | 29.1 | 18.1 | 37.9 |
| Average | 69.9 | | | 27.9 | 17.5 | 36.9 |
| S.D. | 58.6 | | | 4.7 | 2.8 | 6.6 |

[a] Pre-harvest BA = pre-harvest basal area.

[b] Residual BA = residual basal area.

[c] Harvest intensity: *Reference* = woodlots in which no commercial harvesting had taken place for at least 24 years; *Standard* = woodlots containing harvested blocks with residual basal areas within 1.5 m²/ha of the provincial target (20.5 m²/ha) and in which no more than one-third of the total basal area was removed in the most recent cut; *Heavy* = woodlots containing harvested blocks with residual basal areas more than 1.5 m²/ha below the provincial target, or which had more than one-third of their basal areas removed in the most recent cut.

[d] NA = not applicable.

[e] This site had improvement work done through girdling in 1975–1976. These dead trees were removed in 1981–1982.

[f] U = unknown, but not after 1976.

We further classified sites with >1/3 basal area removed as *heavy cut*, regardless of residual basal area measurements (OMNR, 2000).

### 2.2. Field sampling

A single individual (Bradley) conducted all vegetation sampling over a 2-month period, starting in early June of 2001. Within each woodlot vegetation sampling was confined to a single plot, 100 m wide by 200 m long. This 2-ha plot, though randomly located within the treatment, was constrained to a section at least 50 m from the edge of the treatment and woodlot edge, to reduce any confounding influence of edge effects. Records were kept of the species present in all vegetation layers, along with an estimate of abundance. Abundance estimates were scaled as follows: Rare: 1 = 0.1–1% cover, Sparse: 2 = 1–10% cover, Occasional: 3 = 10–25% cover, Common: 4 = 25–60% cover, Abundant: 5 = 60–100% cover. Where abundance estimates were used in data analysis, we took the mean value within the percent cover range for each group (i.e. for species with an abundance estimate of 4, percent cover was given a value of 42.5%). Species encountered outside the transect and plants that could not be identified to species were excluded from the analyses.

Plants were grouped according to the vegetation layer in which they occurred: layer 1 = upper canopy, layer 2 = sub-canopy (>10 m in height), layer 3 = saplings/shrubs 2–10 m in height, layer 4 = regeneration (trees and shrubs 0.5–2 m in height), layer 5 = seedling (shrubs and trees <0.5 m in height), and layer 6 = herbaceous (ferns, forbs, graminoids). For the majority of analyses we focused on the plants occurring in understory layers 5 and 6.

### 2.3. Data analysis

#### 2.3.1. Total plant community

We quantified species richness and abundance and calculated diversity indices for various plant groups including:

number of species across all forest strata (total, native, and non-native), and number of species within the understory (total, native, non-native, herbaceous plants, ferns, trees and shrubs). We calculated diversity based on the Shannon Weiner Index, which accounts for both the number of species and their evenness

Shannon Weiner Index : $(H' = \sum p_i \ln p_i)$

(where $p_i$ is the proportion of species $i$ relative to the total number of species ($p_i$) and ln is the natural logarithm) and the Margalef Index, a measure of community diversity based on the total number of species present and their total abundance

Margalef Index : $D = (S - 1)/\ln N$

where $S$ is the number of species, $N$ the abundance, and ln is the natural logarithm.

We tested the effect of woodlot size, total residual basal area, pre-harvest basal area, residual basal area of medium-sized and larger sawlogs ($\geq$38 cm), proportion loss of basal area for medium-sized and larger sawlogs ($\geq$38 cm), and canopy cover on all dependent variables using step-wise multiple regression analysis. A probability value of 0.20 was the criteria used for entry in the model. Because the consequences of making Type II errors may outweigh those associated with Type I errors when evaluating environmental effects, such as timber harvest (Steidl et al., 1997), all statistical relationships were considered significant at a $p < 0.10$ rather than 0.05 (Schmiegelow et al., 1997).

Plant community composition was described by non-metric multidimensional scaling (NMDS) of species abundance data using PRIMER version 5 software (PRIMER-E Ltd., Plymouth, United Kingdom). NMDS configures samples, in a pre-specified number of dimensions, based on a rank (dis)similarity matrix (Clarke, 1993). We used the Bray-Curtis coefficient calculated on untransformed species data to construct our similarity matrix among samples, and performed independent two-dimensional and three-dimensional ordinations. NMDS was applied in the 'global' form, in which the relative distances apart of all sample points are in rank order agreement with their compositional dissimilarities (Minchin, 1987). The interpretation of the NMDS is simple: points that are closer together on the ordination plot are more similar than points that are farther apart. Statistical differences in plant community composition among treatment groups were determined by an analysis of similarity (ANOSIM; Clarke and Warwick, 1994). ANOSIM is a non-parametric permutation procedure roughly analogous to analysis of variance that tests for separation among a priori-defined groups in ordination space. It is applied to the rank similarity matrix underlying the NMDS ordination.

### 2.3.2. Floristic quality

Each plant was assigned a coefficient of conservatism (CC) score between 0 and 10 for native species, and −1 to −3 for weedy species using the floristic quality assessment system for southern Ontario (Oldham et al., 1995). The coefficient of conservatism score (CC) ranges from 1 to 3 for species found in a wide range of plant communities and under a broad range of disturbance conditions. Species typically associated with woodland habitats, but tolerant of a moderate disturbance were assigned scores between 4 and 6. Values of 9 or 10 were assigned to plants with high degrees of fidelity to a narrow range of synecological parameters (habitat specialists). Weediness scores of −1 were assigned to non-native species that have little or no impact on natural areas, whereas species that have the potential to become a serious problem (i.e. very invasive) were assigned a value of −3. Overall, we tallied the number of native and non-native species, and computed the mean CC and weediness scores for each woodlot (Wilhelm and Masters, 1995). We also computed the Natural Area Index (NAI) by multiplying the mean CC score for all species by the square root of the number of native species (Oldham et al., 1995). As such, woodlots with the highest NAI scores would have a combination of high native species richness and contain species with high CC scores (Wilhelm and Masters, 1995).

## 3. Results

### 3.1. Species richness and diversity

A total of 307 species were identified in all layers across all 19 sites. Of these, 281 (91.5%) were native and 26 were non-native species. There were 210 herbaceous plants (including 32 ferns, 130 forbs, 48 grasses), 44 species of shrub, 41 species of tree, and 12 species of vine. Total species richness varied between sites, ranging from 40 to 124 species, with the majority of species (268 of 307) occurring in the understory. Overall, the residual basal area of medium-sized and larger sawlogs was the strongest predictor of species richness and diversity across most groups, with richness and diversity inversely related to residual basal area (Table 2, Fig. 1). This relationship was particularly evident for herbaceous plants.

We further assessed the relationship between targeted plant groups (understory trees, shrubs, herbaceous species, and ferns) (Table 2). The results showed a strong relationship for herbaceous plants and ferns in terms of richness and diversity, with herbaceous species increasing in richness and diversity with lower RBA of medium sawlogs and larger (herbaceous species richness: $F_{1, 17} = 13.023$, $p = 0.002$; herb $D$: $F_{1, 17} = 11.093$, $p = 0.004$; herb $H'$: $F_{1, 17} = 6.849$, $p = 0.018$) while fern species showed patterns of higher richness and Shannon Weiner diversity in stands with higher pre-harvest basal area measures ($F_{1, 17} = 4.860$, $p = 0.042$; Fern $D$: $F_{1, 17} = 4.281$, $p = 0.055$) and higher diversity using the Margalef index in sites with higher post-harvest BA (Fern $H'$: $F_{1, 17} = 4.923$, $p = 0.041$). Patterns of richness and diversity for understory shrubs and understory trees showed no significant relationship with basal area, canopy cover, or woodlot size measures (Table 2), though there was a tendency for shrub richness to increase with lower canopy cover ($p = 0.24$), and richness of tree species to increase with lower levels of pre-harvest BA ($p = 0.20$). Patterns of richness for shrub and tree species in all layers, however, indicated significantly higher richness in sites

Table 2
Comparison of the key independent variables for each of the measured dependent variables

| Dependent variable | Measure | Independent variable | Relationship | $F$ | $p$ |
|---|---|---|---|---|---|
| Total species | Richness | RBA of medium sawlogs and larger ($M^+$ RBA) | − | 10.832 | 0.004 |
| | $D$ | $M^+$ RBA | − | 11.146 | 0.004 |
| | $H'$ | $M^+$ RBA | − | 4.259 | 0.055 |
| Exotic species | Richness | Pre-harvest BA | − | 6.594 | 0.020 |
| Native species | Richness | $M^+$ RBA | − | 9.727 | 0.006 |
| | $D$ | $M^+$ RBA | − | 9.894 | 0.006 |
| | $H'$ | $M^+$ RBA | − | 4.076 | 0.027 |
| Understory species | Richness | $M^+$ RBA | − | 10.617 | 0.005 |
| | $D$ | $M^+$ RBA | − | 10.668 | 0.005 |
| | $H'$ | $M^+$ RBA | − | 7.573 | 0.014 |
| Herb species | Richness | $M^+$ RBA | − | 13.023 | 0.002 |
| | $D$ | $M^+$ RBA | − | 11.093 | 0.004 |
| | $H'$ | $M^+$ RBA | − | 6.849 | 0.018 |
| Fern species | Richness | Pre-harvest BA | + | 4.860 | 0.042 |
| | $D$ | Post-harvest BA | + | 4.281 | 0.055 |
| | $H'$ | Pre-harvest BA | + | 4.923 | 0.041 |
| Understory tree | Richness | Pre-harvest BA | − | 1.755 | 0.203 |
| Understory shrub | Richness | Canopy cover | − | 1.519 | 0.235 |
| Mean CC | | Canopy cover | + | 4.082 | 0.059 |
| Natural Area Index | | $M^+$ RBA | − | 3.571 | 0.076 |
| Mean weed | | Proportion loss of $M^+$ BA | + | 1.217 | 0.285 |

For each stepwise multiple regression we report the key variables with the strongest influence on the various measures of richness and diversity.

with lower canopy cover (shrub species: $F_{1,\ 17} = 8.726$, $p = 0.009$; tree species: $F_{1,\ 17} = 6.849$, $p = 0.019$).

### 3.2. Native/non-native vegetation

Diversity of native vegetation ranged from 75 to 104 species per site while that of non-natives ranged from 1 to 12 species per site. Only 8.5% of the total species encountered were exotics. Richness of native species in all layers and in the understory decreased significantly with increasing residual basal area of medium-sized and larger sawlogs (all layers: $F_{1,\ 17} = 9.727$, $p = 0.006$; understory: $F_{1,\ 17} = 10.617$, $p = 0.005$).

For non-native species, however, pre-harvest basal area was the best predictor of species richness. As pre-harvest basal area declined, richness of non-native plants increased ($F_{1,\ 17} = 6.594$, d.f. = 1, 17, $p = 0.0199$).

### 3.3. Vegetation quality based on the floristic quality assessment system

Mean coefficients of conservatism (CC) ranged from of 4.713 to 4.939 across treatments and increased significantly with average canopy cover within the stand ($F_{1,\ 17} = 4.082$, $p = 0.059$) (Fig. 2). Hence, as canopy cover increased we see a
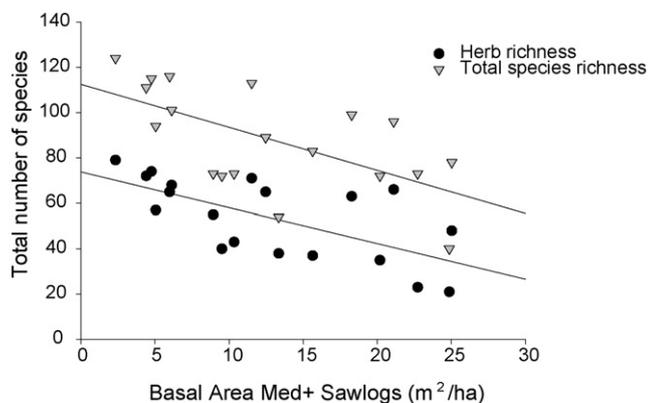


Fig. 1. Linear regression of total number of species across all layers and the total number of herbaceous species in response to residual basal area of all medium-sized and larger sawlogs (≥38 cm dbh). We found a significant decline in species richness with increasing residual basal area (total species richness: $F = 10.83$, $p = 0.004$; herb richness: $F = 13.02$, $p = 0.002$).



Fig. 2. Linear regression between the coefficient of conservatism and the percent canopy cover. Relationship indicates that mean coefficient of conservatism (CC) increases significantly with increasing canopy cover ($F_{1,\ 17} = 4.082$, $p = 0.059$).
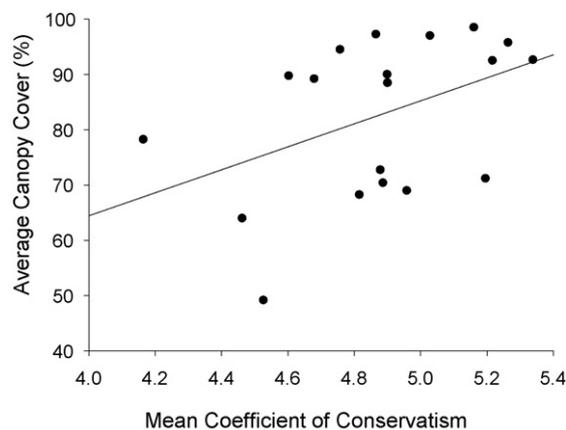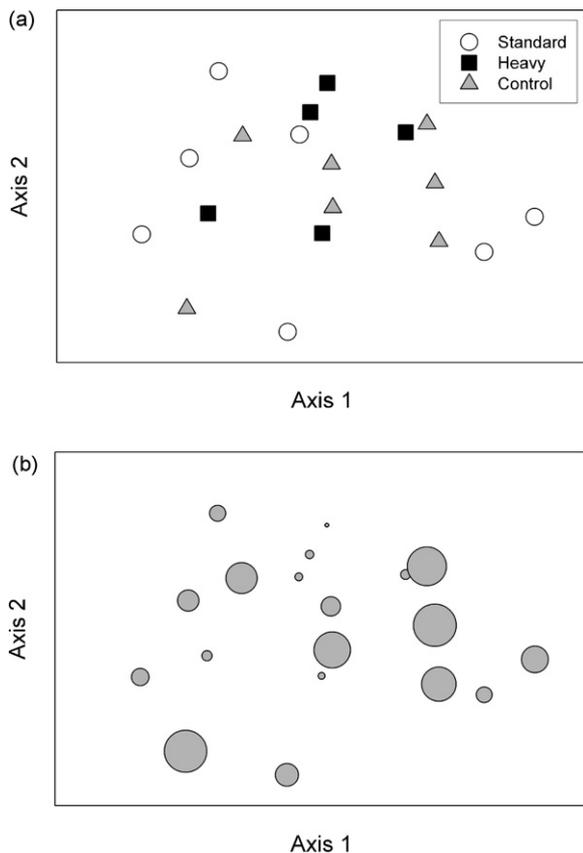
Fig. 3. (a) NMDS ordination of understory vegetation communities based on abundance data. Results show no clear separation of treatments based on composition of the understory plant communities ($R = 0.032$; $p = 0.306$). (b) The same ordination with symbol sizes scaled relative to residual basal area in medium-sized and larger sawlogs. If RBA was important in determining post-harvest plant community composition, you would expect to see a regular pattern (e.g., a clumping of similar-sized bubbles).

pattern of increase in mean CC, and a corresponding increase in forest specialists. However, we found a significant decline in the Natural Area Index with higher RBAs of medium-sized and larger sawlogs ($F_{1,\ 17} = 3.571$, $p = 0.076$). The average weediness scores (WEED) for each treatment ranged from −2.103 to −2.558. WEED scores were not significantly affected by any of the variables measured (Table 2).

Stress values were similar for the two-dimensional and three-dimensional NMDS ordinations (0.16 and 0.10, respectively). Stress is a measure of goodness-of-fit. Since two-dimensional plots are easier to interpret, only the two-dimensional solution is presented here. Overall plant community composition did not differ significantly among the three treatment groups (Fig. 3a; ANOSIM, Global $R = 0.02$, $p = 0.355$). Likewise, there was no obvious relationship between plant community composition and RBA of medium-sized and larger sawlogs (Fig. 3b).

## 4. Discussion

Partial harvesting does have a significant impact on the vegetation in southern Ontario mixed maple woodlands. As

harvesting intensifies, particularly through a loss of trees ≥38 cm dbh (medium sawlogs and larger), we see a significant increase in overall plant richness and diversity. Other studies have documented higher diversity on harvested stands than uncut or reference stands, and increases in diversity after harvest (Crawford, 1976; Metzger and Schultz, 1981; Roberts and Zhu, 2002; Elliott and Knoepp, 2005; Götmark et al., 2005; Zenner et al., 2006; but see Fredericksen et al., 1999). These trends may be linked to changes in canopy cover. Canopy cover has been heralded as one of the most important factors affecting the ground layer vegetation by modifying the site's micro-climate (MacLean and Wein, 1977). Partial harvesting primarily removes canopy trees, and thereby reduces canopy cover. Since the amount and structure of the crown canopy largely influences the composition of the forest understory (MacLean and Wein, 1977), the patchy canopy of partially harvested stands promotes higher herb diversity and better development or immigration of weedy, generalist, or disturbed forest taxa (MacLean and Wein, 1977; Roberts and Zhu, 2002). This, however, may occur at the expense of forest species that are locally uncommon (Roberts and Zhu, 2002) or specialists, and therefore reduce habitat quality. Of all vegetation strata, the understory appears to be most affected by disturbance and micro-environmental change (Meier et al., 1995). As many woodland herbaceous plants tend to be poor at recolonizing a site following disturbances such as harvesting, recent disturbance could eliminate those species adapted to mature undisturbed woodlands. In our study, we found that as the canopy is opened up through a loss of canopy trees, we see a concomitant decrease in forest understory specialists (reduction in mean CC).

The use of the coefficients of conservatism allowed us to account for the effects of harvesting on the vegetation at a level that went beyond richness and diversity measures. Our data indicates that removal of canopy cover through intensive harvesting, may encourage high richness and diversity, but can negatively affect the quality of the vegetation that remains. Though careful selection system harvests may be similar to gap-phase succession in its impacts, it can still result in the displacement of less disturbance-tolerant forest-floor herbs with more disturbance tolerant genera (Meier et al., 1995). Conservation efforts should be mindful of this and focus less strictly on simple biodiversity measures. It is also important to be aware of the impacts of non-native species (Francis et al., 2000) and the overall composition of the vegetation community present when assessing woodland health.

We found that the conditions present on a site before harvest influenced the richness and diversity of the vegetation post-harvest. Previously managed sites, with lower pre-harvest basal areas, tended to have more invasive species, fewer ferns, and greater regeneration of tree species. Many woodland species are slow to recover from disturbances such as logging (Bratton and Meier, 1998), and harvested woodlands may require several centuries to return to their original diversity and composition (Duffy and Meier, 1992). Shade and moisture demanding late successional species, such as many bryophytes and ferns may be particularly vulnerable to the effects of intense management

practices (Roberts and Gillam, 1995; Frisvoll and Presto, 1997; Hannerz and Hanell, 1997; Jalonen and Vanha-Majamaa, 2001; Roberts and Zhu, 2002) and nearly eliminated in clear cuts and retention cuts (Jalonen and Vanha-Majamaa, 2001; Roberts and Zhu, 2002). Where moderate to high basal area and overstory tree cover remains, however, stands are likely to contain high percent cover of these ferns (Fredericksen et al., 1999). Though it is documented that the removal of basal area through logging operations causes the drying out of leaf litter (Harpole and Haas, 1999), soil moisture in partially harvested forests has been shown to increase, at least temporarily, following logging due to the fact that trees and their crowns no longer transpire or intercept the volumes of water and snow that they once did (Barg and Edmonds, 1999; Kranabetter and Coates, 2004). Additional research on these sites actually shows that soil moisture in the spring and fall, at a minimum, is higher in our more heavily cut stands (Burke et al., unpublished data). Hence, recent partial harvest should not pose an immediate effect on moisture demanding plant communities. Once the vegetation grows in, the soil moisture will drop again as the plants consume the water (Gray et al., 2002). Therefore, later intervals since harvest may be more important in shaping patterns of composition of these fern communities when competition for water is more prevalent.

In this study, sites with lower pre-harvest basal areas tended to have more non-native species, indicating that woodlands with a history of intense harvesting could show signs of habitat degradation irrespective of more recent disturbance events. Disturbance increases colonization opportunities (McIntyre et al., 1995), and has been shown elsewhere to favour weedy species (McIntyre and Lavorel, 1994). Most of the managed sites studied here had been subjected to harvesting in the past, and had lower basal areas than reference stands even before the most recent harvest event. Our landscape is heavily fragmented and intensively managed by both private and public land-owners. Very few old-growth forests remain with as little as 0.006% of all the woodland area in southwestern Ontario being considered to be greater than 100 years old in 1986 (OMNR, 1986). All of our reference stands have been logged at some point in the past (as early as 24 years ago). This history of disturbance can have a stronger influence on some floral components than the intensity of recent disturbance events. It is obvious that the vegetation community present in these woodlots many decades ago will play a meaningful role in determining the species composition to date. Future research should investigate the potential for harvesting to result in incremental habitat degradation. Effort should be made to compare old-growth conditions to mature stands with a history of forest management (20–40 years previously) to see how structure and composition vary and how management might alter successional pathways. At present, we are not sure whether successional trajectories will be permanently altered or how long it takes for these harvested stands to return to undisturbed conditions, if ever.

Like Deal (2001), we agree that the plant community structure appears resilient to partial cutting within a moderate range of cutting intensity. Partial cutting is believed to maintain a diverse and abundant plant understory, comparable to plant communities typically found in old-growth stands (Deal, 2001). Harvesting, in fact seems to promote higher diversity overall. Our results support the notion that tree size structure of partially cut stands is an important factor for maintaining understory plant diversity and abundance (Deal, 2001), in particular the amount of basal area of medium-sized and larger sawlogs ($\geq$38 cm dbh) can be a critical factor. However, despite the impacts harvesting had on richness and diversity measures, actual plant community composition was not adequately predicted by residual basal area measures. Like Elliott and Knoepp (2005), we found little similarity in plant species composition based on harvest treatment effects. Instead, we believe that the vegetation is influenced by a more complex combination of measures than were tested here (i.e. site structure, soil type, moisture level, topography, age, disturbance history (grazing, trails, previous logging regimes) (Austin and Smith, 1989; Saunders et al., 1995; Burke and Nol, 1998). Though past management practices are important, and help shape current understory and overstory conditions in managed forests (Halpern and Spies, 1995; Thysell and Carey, 2000; this study) composition of understory plant communities is dynamic and variable between years, even in unmanaged sites.

The longevity of the response of the understory plant community to partial harvest is not well understood. Some researchers have found that ground-layer plant communities are resilient to change and/or recover within 10–15 years post-harvest (Metzger and Schultz, 1984; Jenkins and Parker, 1999; Kern et al., 2006). However, others have found the uneven-aged management using the selection system can shift the communities from species representative of old-growth conditions to weedy and early-successional species (Scheller and Mladenoff, 2002). As such the community composition will be different between stands managed through the selection system and old-growth forests, regardless of actual richness or diversity measures. Uneven-aged management may therefore be problematic in the long term if this disturbance leads to changes in composition characterized by weedy and early-successional species (this study; Scheller and Mladenoff, 2002).

## 5. Conclusion

The relationship between harvest intensity and the response of the herbaceous layer is not well known (Gilliam and Turrill, 1993), though the forest understory remains an ecologically significant component of forest stands. The understory is an important part of wildlife habitat and may substantially affect ecosystem processes like nutrient cycling (Tappeiner and Alaback, 1989). We found that partial harvesting will have a measurable short-term effect on understory plant communities. We caution that assessments of woodland health based on richness and biodiversity measures may encourage more intensive forest management to occur, perhaps at the expense of native forest specialists. Future research should examine which components of biodiversity are negatively affected by

forest management, the timeframe of influence, and how this disturbance over many generations might change the composition and structure of forest ecosystems. Our work and those of others has shown that future management of any stand will invariably affect biodiversity, stand development, and long-term ecosystem structure and function.

## Acknowledgements

## References

Annand, E.M., Thompson III, F.R., 1997. Forest bird response to regeneration practices in central hardwood forests. J. Wildl. Manage. 61, 159–171.

Austin, M.P., Smith, T.M., 1989. A new model for the continuum concept. Vegetatio 83, 35–47.

Barg, A.K., Edmonds, R.L., 1999. Influence of partial cutting on site microclimate, soil nitrogen dynamics, and microbial biomass in Douglas-fir stands in western Washington. Can. J. For. Res. 29, 705–713.

Bratton, S.P., Meier, A.J., 1998. Restoring wildflowers and salamanders in southeastern deciduous forests. Restor. Manage. Notes 16, 158–165.

Burke, D.M., Nol, E., 1998. Edge and fragment size effects on the vegetation of deciduous forests in Ontario, Canada. Nat. Areas J. 18, 45–53.

Chambers, C.L., McComb, W.C., Tappiener Jr., J.C., 1999. Breeding bird responses to three silvicultural treatments in the Oregon Coast Range. Ecol. Appl. 9, 171–185.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143.

Clarke, K.R., Warwick, R.M., 1994. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Plymouth Marine Laboratory, Plymouth, United Kingdom.

Collins, B.S., Pickett, S.T.A., 1987. Influence of canopy opening on the environment and herb layer in a northern hardwood forest. Vegetatio 70, 3–10.

Crawford, H.S., 1976. Relationships between forest cutting and understory vegetation: an overview of Eastern Hardwood Stands. Res. Pap. NE-349. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Upper Darby, PA, p. 9.

Deal, R.L., 2001. The effects of partial cutting on forest plant communities of Western hemlock-Sitka spruce stands in southeast Alaska. Can. J. For. Res. 31, 2067–2079.

Duffy, D.C., Meier, A.J., 1992. Do Appalachian herbaceous understories ever recover from clearcutting? Conserv. Biol. 6, 196–201.

Ehrenfeld, J.G., 1980. Understory response to canopy gaps of varying size in a mature oak forest. Bull. Torr. Bot. Club 107, 29–41.

Elliott, K.E., Knoepp, J.D., 2005. The effects of three regeneration harvest methods on plant diversity and soil characteristics in the southern Appalachians. For. Ecol. Manage. 211, 296–317.

Francis, C.M., Austen, M.J.W., Bowles, J.M., Draper, W.B., 2000. Assessing floristic quality in southern Ontario woodlands. Nat. Areas J. 20, 66–77.

Fredericksen, T.S., Ross, B.D., Hoffman, W., Morrison, M.L., Beyea, J., Johnson, B.N., Lester, M.B., Ross, E., 1999. Short-term understory plant community responses to timber-harvesting intensity on non-industrial private forestlands in Pennsylvania. For. Ecol. Manage. 116, 129–139.

Frisvoll, A.A., Presto, T., 1997. Spruce forest bryophytes in central Norway and their relationship to environmental factors including modern forestry. Ecography 20, 3–18.

Gilliam, F.S., 2002. Effects of harvesting on herbaceous layer diversity of a central Appalachian hardwood forest in West Virginia, USA. For. Ecol. Manage. 155, 33–43.

Gilliam, F.S., Turrill, N.L., 1993. Herbaceous layer cover and biomass in a young versus a mature stand of a central Appalachian hardwood forest. Bull. Torr. Bot. Club 120, 445–450.

Gilliam, F.S., Turrill, N., Adams, M., 1995. Herbaceous-layer and overstory species in clear-cut and mature central Appalachian hardwood forests. Ecol. Appl. 5, 947–955.

Götmark, F., Paltto, H., Nordén, Götmark, E., 2005. Evaluating partial cutting in broadleaved temperate forest under strong experimental control: short-term effects on herbaceous plants. For. Ecol. Manage. 214, 124–141.

Gray, A.N., Spies, T.A., Easter, M.J., 2002. Microclimate and soil moisture responses to gap formation in coastal Douglas-fir forests. Can. J. For. Res. 32, 332–343.

Halpern, C., Spies, T., 1995. Plant species diversity in natural and managed forests of the pacific northwest. Ecol. Appl. 5, 913–934.

Hammond, D.S., Brown, V.K., 1998. Seed size of woody-plants in relation to disturbance, dispersal, soil type in wet neotropical forests. Ecology 76, 2544–2561.

Hannerz, M., Hanell, B., 1997. Effects of the flora in Norway spruce forests following clear-cutting and shelterwood cutting. For. Ecol. Manage. 90, 29–49.

Harpole, D.N., Haas, C.A., 1999. Effects of seven silvicultural treatments on terrestrial salamanders. For. Ecol. Manage. 114, 349–356.

Honer, T.G., Ker, M.F., Alemdag, I.S., 1983. Metric timber tables for the commercial tree species of central and eastern Canada. Canadian Forest Service, Maritimes Forest Research Centre, Information Report M-X-140.

Jalonen, J., Vanha-Majamaa, I., 2001. Immediate effects of four different felling methods on mature boreal spruce forest understorey vegetation in southern Finland. For. Ecol. Manage. 146, 25–34.

Jenkins, M.A., Parker, G.R., 1999. Composition and diversity of ground-layer vegetation in silvicultural openings of southern Indiana forests. Am. Midl. Nat. 142, 1–16.

Kern, C.C., Palik, B.J., Strong, T.F., 2006. Ground-layer plant community responses to even-age and uneven-age silvicultural treatments in Wisconsin northern hardwood forests. For. Ecol. Manage. 230, 162–170.

Kranabetter, J.M., Coates, K.D., 2004. Ten-year postharvest effects of silviculture systems on soil-resource availability and conifer nutrition in a northern temperate forest. Can. J. For. Res. 34, 800–809.

Larson, B.L., Riley, R.L., Snell, E.A., Godschalk, H.G., 1999. The Woodland Heritage of Southern Ontario. Federation of Ontario Naturalists, Don Mills, Ontario.

Lee, H.T., Bakowsky, W.D., Riley, Bowles, J., Puddister, M., Uhlig, P., McMurray, S., 1998. Ecological land classification for southern Ontario: first approximation and its application. Ontario, Ministry of Natural Resources, Southcentral Science Section, Science Development and Transfer Branch, SCSS Field Guide FG-02.

MacLean, D.A., Wein, R.W., 1977. Changes in understory vegetation with increasing stand age in New Brunswick forests: species composition, cover, biomass and nutrients. Can. J. Bot. 55, 2818–2831.

McComb, W.C., Spiers, T.A., Emmingham, W.H., 1993. Douglas-fir forests. Managing for timber and mature-forest habitat. J. For. 91, 31–42.

McIntyre, S., Lavorel, S., 1994. Predicting richness of native, rare, and exotic plants in response to habitat and disturbance variables across a variegated landscape. Conserv. Biol. 8, 521–531.

McIntyre, S., Lavorel, S., Tremont, R.M., 1995. Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. J. Ecol. 83, 31–44.

Meier, A.J., Bratton, S.P., Duffy, D.C., 1995. Possible ecological mechanisms for loss of vernal-herb diversity in logged eastern deciduous forests. Ecol. Appl. 5, 935–946.

Metzger, F., Schultz, J., 1981. Spring ground layer vegetation 50 years after harvesting in Northern hardwood forests. Am. Midl. Nat. 105, 44–50.

Metzger, F., Schultz, J., 1984. Understory response to 50 years of management of a Northern hardwood forest in Upper Michigan. Am. Midl. Nat. 112, 209–223.

Minchin, P.R., 1987. An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio 69, 89–107.

Moore, M.R., Vankat, J.L., 1986. Responses of the herb layer to the gap dynamics of a mature beech-maple forest. Am. Midl. Nat. 115, 336–347.

Norton, M.R., Hannon, S.J., 1997. Songbird response to partial-cut logging in the boreal mixedwood forest of Alberta. Can. J. For. Res. 27, 44–53.

Økland, T., Rydgren, K., Økland, R.H., Storaunet, K.O., Rolstad, J., 2003. Variation in environmental conditions, understorey species number, abundance and composition among natural and managed *Picea abies* forest stands. For. Ecol. Manage. 177, 17–37.

Oldham, M.J., Bakowsky, W.D., Sutherland, D.A., 1995. Floristic Quality Assessment System for Southern Ontario. Natural Heritage Information Centre, Ontario Ministry of Natural Resources, Peterborough, Ontario, Canada.

Ontario Ministry of Natural Resources, 1986. The Forest Resources of Ontario 1986. Ontario Ministry of Natural Resources, Queen's Printer for Ontario, p. 91.

Ontario Ministry of Natural Resources, 2000. A Silvicultural Guide to Managing Southern Ontario Forests, Version 1.1. Ontario Ministry of Natural Resources, Queen's Printer for Ontario: Toronto, p. 648.

Reader, R.J., 1987. Loss of species from deciduous forest understory immediately following selective tree harvesting. Biol. Conserv. 42, 231–244.

Reader, R.J., Bricker, B.D., 1992. Value of selectively cut deciduous forest for understory herb conservation: an experimental assessment. For. Ecol. Manage. 51, 317–327.

Roberts, M.R., Gillam, F.S., 1995. Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. Ecol. Appl. 5, 969–977.

Roberts, M.R., Zhu, L.X., 2002. Early response of the herbaceous layer to harvesting in a mixed coniferous-deciduous forest in New Brunswick, Canada. For. Ecol. Manage. 155, 17–31.

Robinson, W.D., Robinson, S.K., 1999. Effects of selective logging on forest bird populations in a fragmented landscape. Conserv. Biol. 13, 58–66.

Runkle, J.R., 1991. Gap dynamics of old-growth eastern forests: management implications. Nat. Areas J. 11, 19–25.

Saunders, D.A., Hobbs, R.J., Margules, C.R., 1995. Biological consequences of ecosystem fragmentation: a review. Conserv. Biol. 5, 18–32.

Scheller, R.M., Mladenoff, D.J., 2002. Understory species patterns and diversity in old-growth and managed Northern hardwood Forests. Ecol. Appl. 12, 1329–1343.

Schieck, J., Hobson, K.A., 2000. Bird communities associated with live residual tree patches within cut blocks and burned habitat in mixedwood boreal forests. Can. J. For. Res. 30, 1281–1295.

Schmiegelow, F.K.A., Machtans, C.S., Hannon, S.J., 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology 78, 1914–1932.

Simon, N.P.P., Schwab, F.E., Diamond, A.W., 2000. Patterns of breeding bird abundance in relation to logging in western Labrador. Can. J. For. Res. 30, 257–263.

Steidl, R.J., Hayes, J.P., Schauber, E., 1997. Statistical power analysis in wildlife research. J. Wildl. Manage. 61, 270–279.

Steventon, J.D., Mackenzie, K.L., Mahon, T.E., 1998. Response of small mammals and birds to partial cutting and clearcutting in Northwest British Columbia. For. Chron. 74, 703–713.

Tappeiner, J.C., Alaback, P.B., 1989. Early establishment and vegetative growth of understory species in the western hemlock—Sitka spruce forests of southeast Alaska. Can. J. Bot. 67, 318–326.

Thompson, J.N., 1980. Treefalls and colonization patterns of temperate forest herbs. Am. Midl. Nat. 104, 176–184.

Thysell, D.R., Carey, A.B., 2000. Effects of forest management on understory and overstory vegetation: a retrospective study. United States Department of Agriculture and Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-488, p. 41.

Wilhelm, G.S., Masters, L.A., 1995. Floristic Quality Assessment in the Chicago Region and Application Computer Programs. The Morton Arboretum, Lisle, Ill.

Zenner, E.K., Kabrick, J.M., Jensen, R.G., Peck, J.E., Grabner, J.K., 2006. Responses of ground flora to a gradient of harvest intensity in the Missouri Ozarks. For. Ecol. Manage. 222, 326–334.