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Effects of single-tree and group selection harvesting on the diversity and abundance of spring forest herbs in deciduous forests in southwestern Ontario

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Abstract

Selection harvesting, by mimicking natural disturbance regimes of eastern deciduous hardwood forests, has been applied as a sustainable management practice that combines wood production with biodiversity conservation. However, the effects of this technique on understory herbs are unclear, particularly for spring ephemerals which have been suggested as sensitive to disturbance. Here, we experimentally assess the immediate effects of single-tree and group selection harvesting on spring ephemeral richness, diversity and abundance in deciduous forests of southwestern Ontario, Canada. Spring herbs were quantified in 4 m² plots before and one growing season after harvesting and compared to similar uncut, reference stands. The percent of species lost was significantly higher in reference than harvested plots. Mean species richness significantly increased after harvesting, predominately due to an increase in spring–summer species. Increases in the diversity of early spring flowering species were significantly greater in the group selection plots than reference plots. At the community level, no species appeared to be vulnerable to harvesting, and ordination analysis indicated that post-harvest communities were primarily determined by pre-harvest community composition. Furthermore, no species declined in abundance in response to harvesting, and overall percent cover increased proportionately more in single-tree selection plots than in group selection or reference plots. While harvesting appears to have negligible effects on spring ephemerals immediately following harvest, we recommend additional studies over longer time frames to assess possible successional effects and to discriminate treatment induced changes from naturally high yearly variation in species composition.

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1. Introduction

As forests across North America continue to be fragmented and influenced by human activities, the importance of maintaining biodiversity has become widely recognized (Millar et al., 1990; Burton et al., 1992). This is particularly evident in southwestern Ontario where only 3% forest cover remains in some counties. An estimated 87% of the remnant forest is privately owned and managed according to a variety of landowner objectives, with commercial timber harvesting being a dominant land-use practice (OMNR, 2000). Consequently, determining whether current harvesting practices are sustain-

able and what silviculture methods best meet landowner objectives while still maintaining a healthy ecosystem is of increasing importance.

In the deciduous forests of eastern North America, woodland herbs account for most of the vascular plant diversity (Whigham, 2004). They play a vital role in ecosystem functioning, particularly in nutrient cycling (MacLean and Wein, 1977; Peterson and Rolfe, 1982; Anderson and Eickmeier, 2000). Of all vegetation strata, the understory is affected most by disturbance and micro-environmental change (McCarthy and Facelli, 1990; Meier et al., 1995). In particular, spring ephemerals or ‘vernal’ herbs which are visible on the forest floor before overstory canopy closure in late spring (Meier et al., 1995), have been identified as a group of plant species highly vulnerable to disturbance (Duffy and Meier, 1992; Keddy and Drummond, 1996; McLachlan and Bazely, 2001).

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A considerable amount of research has addressed the response of understory herbs to harvesting, particularly in response to clear-cutting (Duffy and Meier, 1992; Gilliam et al., 1995; Halpern and Spies, 1995; Meier et al., 1995; Gilliam, 2002; Roberts and Zhu, 2002; Small and McCarthy, 2002a; Pykala, 2004). Some researchers have found no significant difference in species richness and composition between cut and uncut stands 20+ years post-harvest (Metzger and Schultz, 1984; Gilliam et al., 1995; Gilliam, 2002), while others have found that herb communities are negatively affected by clear-cut logging (Halpern and Spies, 1995; Scherer et al., 2000) and may take >50 years to recover (Duffy and Meier, 1992; Meier et al., 1995). The lack of consistency in findings demonstrates the possible system-specific nature of herb-layer responses (Halpern and Spies, 1995) and the need for further research into the understory dynamics of forest communities (Matlack, 1994; Whigham, 2004).

Selection harvesting has been applied as a sustainable alternative to clear-cut harvesting in forests dominated by shade-tolerant species (Reader, 1987; Fredericksen et al., 1999). By mimicking natural gap-phase dynamics and small-scale disturbance regimes, selection harvesting creates heterogeneous stand structures similar to mature forests (Deal, 2001; Deal and Tappeiner, 2002) and is likely to have fewer negative impacts on forest biodiversity than clear-cut harvesting (Reader and Bricker, 1992b; Meier et al., 1995). In southern Ontario selection harvesting is recommended for most broadleaf forests (OMNR, 2000). Depending on forest composition and objectives, selection harvests can be designed to remove single trees, groups of trees or a combination of the two. In single-tree selection, harvesting to a target residual basal area is achieved by removing individual trees from a range of diameters throughout an entire stand. In contrast, group-selection is used to encourage the regeneration of mid-tolerant species and involves removing trees in patches (up to 50 m in diameter) to create forest gaps.

Selection harvesting differs from natural gap dynamics in several ways, including: the scale and frequency of disturbance; woody debris removal; soil structure from compaction and erosion by logging equipment; and direct surface disturbance such as trampling (Bratton, 1994). All of these differences have the potential to affect understory herbaceous communities in both positive and negative ways (Reader, 1987; Hughes, 1992; Whigham, 2004; Scheller and Mladenoff, 2002; Small and McCarthy, 2002a).

Despite the complexity of responses to changes in their environment, herbs appear to be resilient to the effects of single-tree selection harvesting (Fredericksen et al., 1999; Deal, 2001; Gotmark et al., 2005). Yet, few studies have compared the understory of harvested gaps to the understory of undisturbed canopy (e.g., Metzger and Schultz, 1984; Collins and Pickett, 1987; Jalonen and Vanha-Majamaa, 2001; Schumann et al., 2003) and even fewer have compared single-tree to group selection with regard to spring herb diversity (e.g., Metzger and Schultz, 1984; Jalonen and Vanha-Majamaa, 2001). Given that group selection creates very different light environments than single-tree selection, and that

light strongly influences herb layer diversity, the impacts of these two harvesting prescriptions on spring herbs in southern Ontario are likely to differ. Furthermore, Gotmark et al. (2005) found that the herb layer is highly dynamic in the short-term and recognized the need for experiments with strong temporal control (i.e. before-after studies) to measure direct effects.

We compared the impacts of single-tree and group selection harvesting on spring herb communities by evaluating harvesting effects on: (1) loss of species, (2) richness, diversity and evenness, (3) changes in community composition, and (4) frequency and abundance of individual species that are potentially sensitive to disturbance. We hypothesized that most species would respond positively to harvesting and overall richness and diversity would increase in harvested plots. However, those species identified as sensitive to disturbance would decrease or even be locally extirpated by harvesting, and these species-specific responses could alter community composition.

2. Methods

2.1. Study area

The study took place in six woodlots within Norfolk and Middlesex counties, southern Ontario, Canada (~42°42'N, 81°81'W). This area marks the northernmost edge of the Carolinian deciduous forest region and contains a number of species found nowhere else in Canada (Fox and Soper, 1955). Woodlots ranged in size from 97 to 270 ha and were embedded in an intensive agricultural matrix (14–25% forest cover). Dominant canopy species included: red maple (*Acer rubrum* L. 17% basal area (BA)), red oak (*Quercus rubra* L. 13% BA), silver maple (*Acer saccharinum* L. 12% BA), white oak (*Quercus alba* L. 7% BA), freeman maple (*Acer freemanii* A. E. Murray 6% BA), sugar maple (*Acer saccharum* Marsh. 6% BA), and green ash (*Fraxinus pennsylvanica* Fern. 5% BA).

2.2. Woodlot selection and harvesting

Woodlots with similar stand structure (i.e. basal area and canopy closure) and species composition were selected for study. All woodlots had previously been harvested prior to the late 1970s, but had returned to a mature, closed canopy stand structure before the application of our treatments. Two replicates from each of three treatments were studied — 2 woodlots harvested under single-tree selection, 2 woodlots harvested under group selection, and 2 reference woodlots left unharvested (3 treatments × 2 replicates = 6 woodlots). Treatment areas were similar in size (average = 32.9 ± 3.9 ha). Within each group selection woodlot, 5 small (400 m²) and 4 medium (700 m²) gaps were intermixed and spread across one half of the treatment area and 3 large (1400 m²) gaps were spread across the other half of the treatment area. Individual gap locations were chosen based on silviculture principles for regenerating mid-tolerants with the caveat that they be at least 50 m from the edge of the forest (to reduce the possibility of confounding edge effects due to proximity to hard edges) and at

least 20 m from each other (edge to edge). The intervening matrix within the group selection treatment area was left unharvested. In single-tree selection woodlots, marking for single-tree selection was applied uniformly across the treatment area to a target residual BA of 20 m²/ha. Harvesting occurred between November 2004 and April 2005. Overall, basal area decreased by 5% in the group selection treatment, 18% in the single-tree selection treatment, and increased by 3.6% in the reference treatment one year post-harvest.

2.3. Vegetation sampling

In each single-tree selection and reference woodlot, 15 circular permanent growth plots (PGPs) of 400 m² were established 100 m apart from each other along 2–3 transects. Transects varied in length and orientation due to restrictions imposed by the treatment area size and shape, but were spread uniformly across the treatment area and arranged such that each PGP center was at least 50 m away from an adjacent PGP plot center, and was typically 100 m apart in all directions. In a similar manner, 12 PGPs were spread across the uncut portion of each group selection woodlot. For all single-tree selection woodlots, reference woodlots, and uncut sections of group selection woodlots (G_u) three circular 4 m² regeneration growth plots (RGPs) were embedded within each PGP, 5 m from the plot centre in a triangular formation (120 degrees apart). As such, a total of 45 RGPs were measured in single tree selection and reference woodlots, and 36 in uncut sections of group selection woodlots. Additional RGPs were measured within gaps in the group selection woodlots, with each RGP being a minimum distance of 5 m from adjacent RGPs. Five, 6 and 9 plots were established within each small, medium and large group selection gap size respectively, for a total of 76 within-gap (G_g) RGPs per group selection woodlot. The spatial arrangement of RGPs within PGPs and gaps is shown in Fig. 1.

All spring-flowering herb species were identified within each RGP after snow melt in the early spring. For each species the number of stems was counted and percent cover estimated.

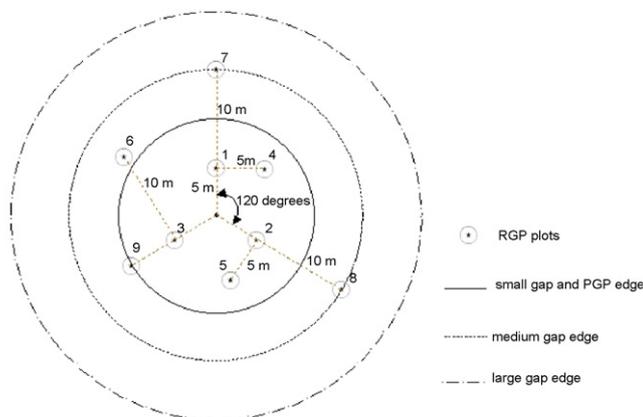


Fig. 1. Layout of regeneration plots (RGPs) within gaps and permanent growth plots (PGPs). RGP #1 was placed at random azimuth from the plot center and all other RGPs were orientated respectively. PGPs contain RGPs #1–3; small gaps contain RGPs #1–5; medium gaps contain RGPs #1–6; and large gaps contain RGPs # 1–9.

The percent of each plot disturbed by logging, i.e. having either exposed, compacted or shifted soil, or logging debris, was estimated post-harvest. Sampling was conducted between 19 April and 30 April 2004 prior to harvesting, and immediately following harvesting between 27 April and 5 May 2005. Sampling was carried out at a later date post-harvest because of a later spring thaw.

2.4. Data analysis

Due to the early sampling time frame and the inherent variability in sampling herbaceous communities (Small and McCarthy, 2002b) some herbaceous species were not well represented during our sampling period. Therefore, species were grouped based on seasonal growing patterns observed in the study, i.e. those with early-spring foliage die-off (early die-off), those species widespread in early spring (early spring), and all species present, but not yet widespread, in the early spring (mid-spring). Presence/absence records for each plot from plant surveys during the summer were combined with our spring data to get a more accurate picture of mid-spring species composition. Finally, species that would potentially respond negatively to disturbance, as determined by a literature review, were grouped together (sensitive species). A list of all species contained within each species group can be found in Appendix A.

The percent of species lost and gained, species richness, diversity and evenness were calculated for each plot and averaged across woodlots. Species loss and gain were expressed as percents because preliminary analysis revealed that pre-harvest richness was significantly different between treatments ($P = 0.012$) (e.g. Reader, 1987). Species richness was a count of the number of species per plot. Species diversity was calculated using the ln-based Shannon index (H') and evenness using Pielou's evenness index (J') (Zar, 1996). However, since plot species richness was low for early-die off and sensitive species, and abundance measures were not available for all mid-spring species, H' and J' were only calculated for early-spring species. Species loss and gain were compared among treatments with one-way analysis of variance (ANOVA) models with plots nested in woodlots, and Tukey multiple comparison tests were used to identify where significant differences among treatment means occurred (Zar, 1996). Correlation analysis and Pearson product-moment correlation coefficients were used to evaluate the relationship between percent logging disturbance and percent of species lost and gained by plot. Richness, diversity, and evenness were compared among treatments using two-way repeated measures ANOVA models (Zar, 1996) with plots nested in woodlot. We considered significant interactions between year (before-after) and treatment (reference, group, single-tree) to indicate a harvest effect. When a significant interaction was found all possible treatment comparisons were examined to determine which treatments differed from each other. Since preliminary analysis revealed that patterns of change were not significantly different between G_g and G_u plots ($P > 0.10$), these plots were pooled for the group selection treatment. For analysis, all

percents and counts were arcsine and square root transformed, respectively, to meet the assumptions of normality (Zar, 1996). For all statistical tests differences between treatments were assumed to be significant at $P < 0.10$, to minimize Type II errors. Analyses were conducted using S-Plus 6.1 software.

Differences in forest plant community composition among treatments were analyzed by non-metric multidimensional scaling (NMDS) of species composition using PRIMER version 5 software (PRIMER-E Ltd., Plymouth, United Kingdom), as described by Clark and Warwick (1994).

At the species level, changes in the frequency of occurrence (proportion of plots where the species was detected) from before to after harvest were compared between treatments using G -tests for those species present at an average expected frequency > 6 (Zar, 1996). Changes in abundance for all species combined, and for a subset of species that were sufficiently sampled and potentially sensitive to disturbance, were compared between treatments using repeated measures ANOVA models as outlined above. Individual species examined included *Trillium grandiflora*, *Trillium* spp. (*T. grandiflora* and *T. erectum* combined) *Anemone quinquefolia*, *Erythronium americanum*, *Claytonia virginica*, *Carex pennsylvanica* and *Viola pubescens* (Metzger and Schultz, 1981; Moore and Vankat, 1986; McLachlan and Bazely, 2001).

3. Results

Treatment had a significant effect on the percent of species lost ($P = 0.028$). The percent of species lost per plot was significantly higher in the reference ($14.8 \pm 2.4\%$) compared to the group selection treatment ($8.4 \pm 1.1\%$), but similar to the single-tree selection treatment ($11.1 \pm 2.2\%$). Percent of species gained per plot was similar among treatments: reference ($28.6 \pm 4.7\%$), group selection ($34.6 \pm 3.1\%$) and single-tree selection ($42.1 \pm 6.0\%$).

Harvesting had a significant effect on the species richness of mid-spring herbs (Table 1) and the diversity of early-spring herbs (Table 2). Species richness increased significantly post-harvest in the single-tree selection treatment ($P = 0.003$) and the group selection treatment ($P = 0.02$) compared to the reference treatment. Diversity increased significantly ($P = 0.02$) post-harvest only in the group selection treatment compared with the reference treatment. Harvesting had no effect on evenness.

Logging disturbance was significantly higher in group selection plots ($50 \pm 2.8\%$) than in single-tree selection plots ($16 \pm 3.4\%$) ($P < 0.001$). However, there was no significant correlation between percent of logging disturbance and percent of species lost or gained.

Post-harvest communities were determined primarily by their pre-harvest species compositions (Fig. 2). Two species were found to increase in frequency of occurrence following harvesting, *Claytonia virginica* and *Viola sororia* (Table 3). No species decreased in frequency or were consistently lost from harvested plots (Table 3). *Sanguraina canadense* was confined to reference woodlots so the effects of harvesting on this uncommon species could not be determined.

Table 1

Total species and mean \pm standard error species richness by plot for each species group shown by treatment

	No. plots ^a	No. species		Mean richness	
		Pre	Post	Pre	Post
Mid-spring					
Single-tree	90	28	31	3.6 \pm 0.2	4.5 \pm 0.3 ^a
Group	224	29	34	3.7 \pm 0.1	4.4 \pm 0.2 ^{ab}
Reference	90	26	28	4.3 \pm 0.3	4.8 \pm 0.3 ^b
$F = 5.17, P = 0.006$					
Early spring					
Single-tree	77	13	15	1.5 \pm 0.1	2.0 \pm 0.2
Group	203	19	22	1.1 \pm 0.1	1.5 \pm 0.1
Reference	75	15	17	2.3 \pm 0.3	2.6 \pm 0.3
$F = 0.07, P = 0.93$					
Sensitive species					
Single-tree	90	8	8	1.7 \pm 0.1	2.0 \pm 0.2
Group	224	7	8	1.7 \pm 0.1	1.9 \pm 0.1
Reference	90	8	8	2.0 \pm 0.1	2.1 \pm 0.2
$F = 1.24, P = 0.29$					
Early die-off					
Single-tree	77	4	5	0.5 \pm 0.1	0.7 \pm 0.1
Group	203	5	6	0.5 \pm 0.0	0.8 \pm 0.1
Reference	75	4	5	1.2 \pm 0.1	1.5 \pm 0.2
$F = 0.33, P = 0.72$					

Significant differences among treatments are denoted in bold. Treatment means sharing the same letter are not significantly different.

^a Plots flooded with water in the early spring were excluded from early spring and early die-off data sets. Mid-spring and sensitive species data sets included data from the summer when the plots were dry.

Harvesting had a significant positive effect on the total percent cover of all forest herb species combined ($P = 0.09$), and the abundances of *Anemone quinquefolia* ($P = 0.03$), *Trillium* spp. ($P = 0.03$) and *Viola pubescens* ($P < 0.001$) (Fig. 3). *Trillium* spp. and *V. pubescens* declined in abundance in the reference treatment, but increased in both harvest treatments. *A. quinquefolia* declined in abundance on reference and group selection treatments compared with the single-tree selection treatment. Abundances of *Trillium grandiflora*, *Erythronium americanum*, *Claytonia virginica* and *Carex pennsylvanica* were unaffected by harvesting.

4. Discussion

Our results indicate that disturbance associated with single-tree selection and group selection harvesting does little to alter

Table 2

Mean (\pm standard error) species diversity and evenness of the early spring species by treatment and year

Treatment	H'		J'	
	Pre	Post	Pre	Post
Single-tree	0.19 \pm 0.03	0.26 \pm 0.04 ^{bc}	0.40 \pm 0.05	0.28 \pm 0.04
Group	0.15 \pm 0.02	0.25 \pm 0.03 ^a	0.32 \pm 0.03	0.27 \pm 0.03
Reference	0.32 \pm 0.05	0.34 \pm 0.04 ^c	0.27 \pm 0.04	0.26 \pm 0.03
Harvest \times Treatment	$F = 2.4, P = 0.09$		$F = 2.0, P = 0.14$	

Treatment means sharing the same letter are not significantly different.

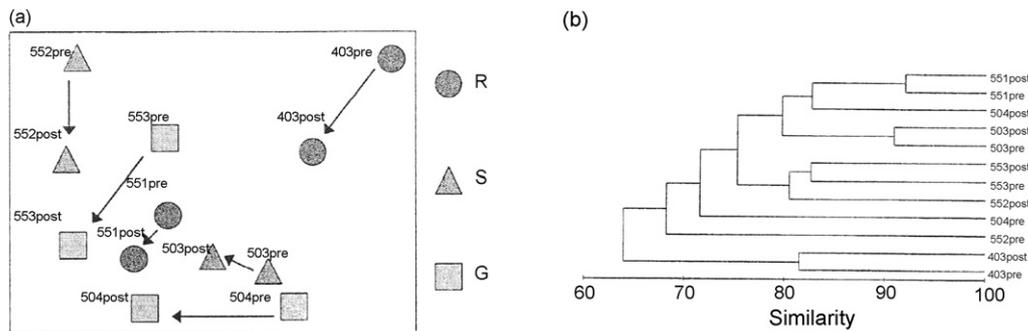


Fig. 2. NMDS (a) and similarity ordination analysis (b) of spring herb community composition pre and post-harvest by treatment. Different symbols represent reference (R), single-tree selection (S) and group selection (G) treatments. Woodlots are identified by number and harvest period (pre/post).

the persistence of spring ephemeral herbs in the first growing season after logging. In fact, the average number of species lost from plots was greatest in the reference treatment. This is likely due to the timing of harvesting. During the winter, meristems of herbaceous plants are below the snow surface which may protect them from the surface disturbance associated with harvesting (Reader, 1987; Schumann et al., 2003). Other studies have similarly found no significant differences in the loss of herbaceous species following harvest between unharvested and selectively logged stands (Reader, 1987; Gotmark et al., 2005).

In general, species richness and diversity increased with harvesting. This is consistent with the results of other studies that found increased species richness and diversity associated with single-tree selection harvesting immediately following harvest (*maple forest*: Metzger and Schultz, 1981; *oak forest*: Gotmark et al., 2005), or a tendency for higher species richness in harvested gaps 1–2 years (*European beech forest*: Gálhidy et al., 2006) and 5 years (*oak-pine forest*: Schumann et al., 2003) post-harvest. Similar responses are associated with natural gap-phase dynamics (*oak-hickory forest*: Thompson, 1980; *black cherry-maple forest*: Collins and Pickett, 1987). Local increases in species richness are likely due to increases in environmental heterogeneity (Vellend et al., 2000) creating niches that favour the establishment of species not present prior to harvest. Soil disturbance creates new colonization sites for species present locally (within 1 m) that are able to disperse effectively and exploit unused resources rapidly (Thompson, 1980; McIntyre et al., 1995). Changes in microclimate conditions (increases in light and release of nutrients) may stimulate regeneration of species that form persistent soil seed banks (Mladenoff, 1990; Pykala, 2004; Gotmark et al., 2005). In the single-tree selection treatment, large increases in richness were paralleled by large decreases in evenness resulting in less change in diversity, whereas in group selection plots increases in richness outweighed decreases in evenness, resulting in significant increases in diversity. This suggests that species gained in the group selection treatment were generally more abundant than species gained in the single-tree selection treatment (Small and McCarthy, 2002b). At the species level, increases in richness post-harvest were caused primarily by increases in the frequencies of species already present on the site, in particular *Claytonia virginica* and *Viola sororia*. Canopy opening is likely to have a greater effect on spring-summer

herbs, like *Viola* spp. (Ristau et al., 2001) than early spring herbs since differences in environmental conditions between gaps and intact canopy are not as distinct in the early spring when canopy leaf out is only just beginning, resulting in less pronounced microclimate effects on early spring herbs (Moore and Vankat, 1986). This is likely why significant post-harvest increases in richness were seen only in the mid-spring herbs which represented a larger proportion of spring–summer species. The observed increase in the frequency of *C. virginica* in group selection plots may be attributed to increases in nutrients levels caused by harvesting (Anderson and Eickmeier, 1998). *C. virginica* is a shade-intolerant species that has been shown to be a strong competitor in gaps and open environments (Rogers, 1982; Moore and Vankat, 1986).

Despite increases in some species following harvesting, ordination showed that post-harvest communities were strongly determined by pre-harvest communities with no underlying patterns due to harvesting. Hughes and Fahey (1991) similarly found that the spatial distribution of herbs following canopy removal in northern hardwood forests, were strongly determined by herb layer composition pre-disturbance. No species was negatively affected by either single-tree or group selection harvesting. The richness of species considered sensitive to disturbance did not decrease at a higher rate due to harvest. In fact, the number of these species tended to increase after harvest, although this increase was not significant. We were unable to assess the effects of harvesting on *Sanguinaria canadensis*, a rare, late successional, shade intolerant species potentially sensitive to disturbance (Elliott et al., 1997). Its absence from all woodlots prior to harvest may have been the failure of our plot-based sampling to detect infrequent species (Ristau et al., 2001). We suggest further, targeted sampling may be needed to detect the response of this and other rare species to disturbance.

Percent cover of all species combined, and the abundances of *Anemone quinquefolia*, *Trillium* spp. and *Viola pubescens*, responded positively to harvesting. Increased light and nutrients were the likely drivers of this positive response to harvest (Moore and Vankat, 1986). It was expected that populations of mesic herbs adapted to moist, low-competition conditions (e.g., *Erythronium americanum*, *Claytonia virginica*) or with slow population growth (e.g., *Trillium grandiflora*) would suffer reduced populations in response to harvesting, through competition with faster-growing, annuals

Table 3
No. of plots each species was detected present (frequency) pre and post harvest by treatment

Species	Reference		Group		Selection		χ^2 ^a	P
	Pre	Post	Pre	Post	Pre	Post		
<i>Allium tricoccum</i>	3	3	1	3	1	0		
<i>Anemone Americana</i>	0	0	2	0	1	3		
<i>Anemone quinquefolia</i>	16	16	48	50	4	8	1.1	0.564
<i>Arisaema triphyllum</i>	44	30	27	26	30	26	1.0	0.609
<i>Caltha palustris</i>	0	0	4	4	0	0		
<i>Cardamine diphylla</i>	0	14	0	5	0	0		
<i>Cardamine douglassii</i>	0	0	10	3	1	0		
<i>Carex blanda</i>	1	1	6	9	2	1		
<i>Carex communis</i>	0	0	0	0	1	1		
<i>Carex laxiflora</i>	4	3	0	0	0	1		
<i>Carex pedunculata</i>	0	6	0	3	0	0		
<i>Carex pensylvanica</i>	6	8	48	56	11	10	0.4	0.832
<i>Carex spp.</i> ^b	17	32	60	108	20	46	0.6	0.730
<i>Caulophyllum thalictroides</i>	1	1	0	1	1	1		
<i>Claytonia virginica</i>	32	35	1	29	3	2	15.7	0.000
<i>Erythronium americanum</i>	40	37	48	48	35	34	0.1	0.968
<i>Geranium maculatum</i>	13	13	58	77	31	31	1.1	0.588
<i>Hydrophyllum virginianum</i>	0	1	0	3	0	0		
<i>Maianthemum canadense</i>	41	55	144	153	36	46	1.3	0.535
<i>Maianthemum racemosum</i>	32	34	76	80	35	43	0.3	0.847
<i>Mitella diphylla</i>	0	0	6	5	0	1		
<i>Osmorhiza claytoni</i>	17	19	64	75	2	1	0.5	0.774
<i>Podophyllum peltatum</i>	7	7	8	9	14	15	0.0	0.987
<i>Polygonatum pubescens</i>	37	38	97	99	22	24	0.0	0.979
<i>Ranunculus abortivus</i>	1	0	7	11	8	8		
<i>Sanguinaria canadensis</i>	3	3	0	0	0	0		
<i>Symplocarpus foetidus</i>	3	2	15	13	11	10	0.1	0.953
<i>Tiarella cordifolia</i>	1	2	13	12	4	6	0.7	0.713
<i>Trillium erectum</i>	13	15	10	11	11	11	0.1	0.969
<i>Trillium grandiflora</i>	22	21	47	47	26	24	0.1	0.973
<i>Trillium spp.</i> ^b	41	46	69	73	40	47	0.2	0.926
<i>Uvularia sessilifolia</i>	2	10	5	23	0	10	3.4	0.182
<i>Viola blanda</i>	5	2	10	8	2	2		
<i>Viola canadensis</i>	0	0	2	3	1	3		
<i>Viola conspersa</i>	1	1	11	7	2	7		
<i>Viola macloskeyi</i>	0	0	1	2	0	0		
<i>Viola pedata</i>	0	0	0	4	0	4		
<i>Viola pubescens</i>	23	27	15	16	12	10	0.4	0.800
<i>Viola sororia</i>	14	3	18	22	10	12	8.0	0.018
<i>Viola spp.</i> ^b	44	35	58	78	31	46	4.6	0.100

Likelihood G-tests were used to test for independence between treatment group and sampling period. Significant results are in bold.

^a Significance tests were only performed on those species that had an average expected frequency (n/rc) > 6.0 as suggested by Zar (1996).

^b Species grouped into genera because non-flowering plants could not be reliably distinguished into separate species. Genera groups included all species identified and all species unidentifiable.

or ruderals adapted to high-light or xeric conditions (Rogers, 1982; Meier et al., 1995; Bratton and Meier, 1998). However, this was not the pattern we observed. There may be delayed species-specific responses (Rogers, 1983; Collins and Pickett, 1987; Williams and Bricker, 1992) that we did not detect in our short-term study (Hughes, 1992; Reader and Bricker, 1992a; Meier et al., 1995). Furthermore, natural annual variability in abundance may have masked treatment induced changes (Kennedy and Addison, 1987; Oekland, 1995; Jalonen and Vanha-Majamaa, 2001).

Differences in species richness, diversity and community composition between single-tree and group selection treatments were minor. Jalonen and Vanha-Majamaa (2001) also found that changes in vegetation response were similar between

stands treated with multiple-tree gap felling and single-tree selection. Furthermore, Reader and Bricker (1992a) studied the response of five forest herb species to partial harvesting and found that herb frequency was not likely to increase in large canopy openings versus smaller canopy openings.

In summary, selection harvesting does not appear to have strong negative impacts on spring ephemeral herbaceous plant communities in the first growing season after harvest. No species were lost, or reduced in frequency or abundance as a result of single-tree or group selection harvesting. Although harvesting increased the frequency of occurrence of some spring–summer species like *Viola spp.*, components of the original understory continued to dominate the post-harvest community.

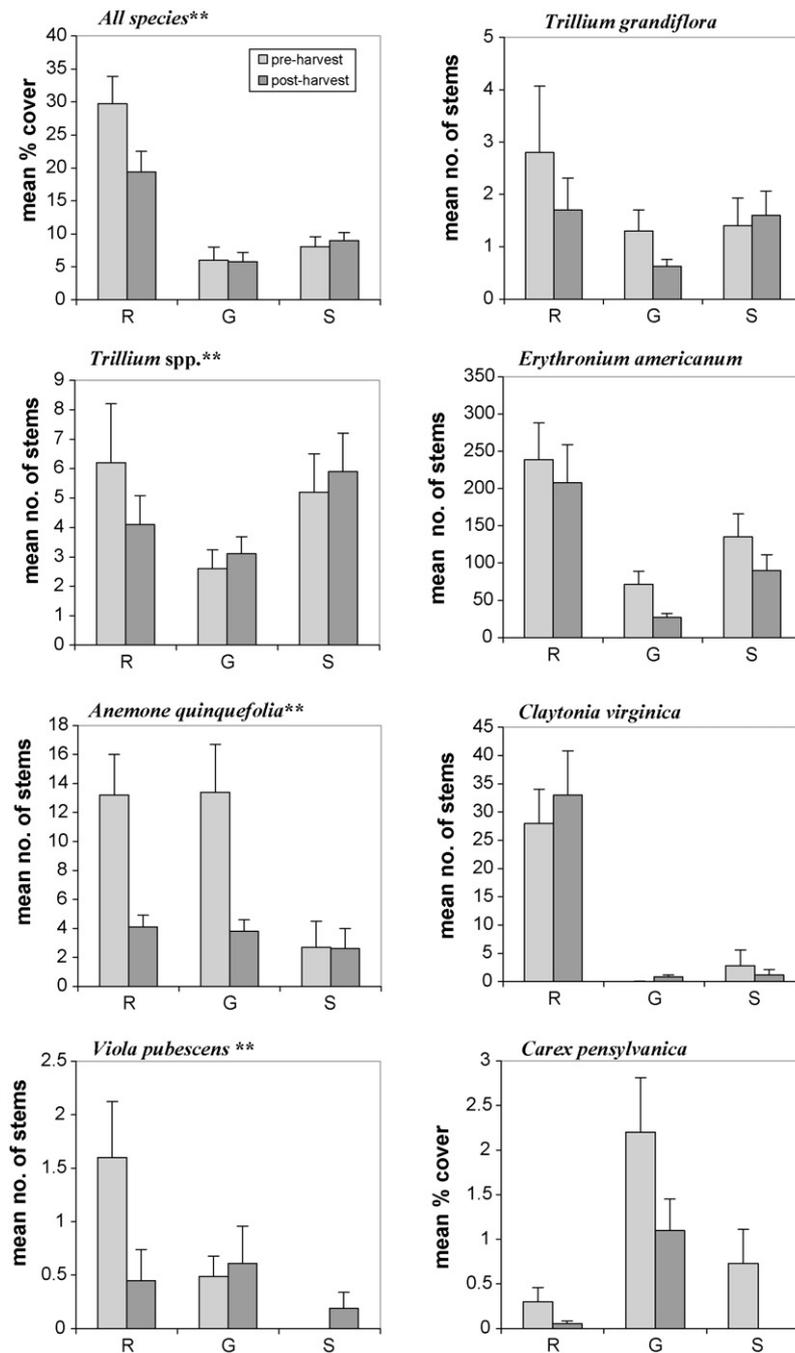


Fig. 3. Mean abundance by treatment (R = reference; G = group selection; S = single-tree selection) before and after harvest for selected species. Significant interactions between treatment \times year indicated with double asterisks (**). Mean% cover was used to describe all species combined, as a more accurate representation of total plant abundance than number of stems.

While the immediate effects of single-tree and group selection harvesting on species richness and community composition appear to be minimal, some responses may be delayed and take multiple growing seasons to become apparent. As succession takes place, populations of some spring herbs may decrease due to their inability to adapt to microclimatic change or compete with other species more suited to the new microenvironment (Hughes, 1992; Reader and Bricker, 1992a; Meier et al., 1995). Since species were not locally extirpated by harvesting, barriers to recovery of vernal herbs, like slow

dispersal, growth and reproduction (Meier et al., 1995) are not likely to play a strong role in longer-term effects. However, the ecological implications of reduced populations of spring herbs could be substantial, as these plants play a large role in nutrient uptake and cycling (MacLean and Wein, 1977; Peterson and Rolfe, 1982; Anderson and Eickmeier, 2000). We suggest further sampling in subsequent years to assess successional responses of individual species and to better discriminate treatment effects from the naturally high annual variation that occurs in herbaceous communities.

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Appendix A. List of spring herbs in the six study woodlots in Norfolk and Middlesex counties, Ontario, grouped by phenology and sensitivity to disturbance

	Mid-spring	Early spring	Early die-off	Sensitive species ^a
<i>Allium tricoccum</i>	✓	✓		
<i>Anemone quinquefolia</i>	✓	✓	✓	
<i>Anemone Americana</i>	✓	✓		
<i>Arisaema triphyllum</i>	✓			✓
<i>Caltha palustris</i>	✓	✓		
<i>Cardamine</i> spp.	✓	✓		
<i>Cardamine diphylla</i>	✓	✓	✓	
<i>Cardamine douglassii</i>	✓	✓	✓	
<i>Carex blanda</i>	✓			
<i>Carex communis</i>	✓			
<i>Carex laxiflora</i>	✓			
<i>Carex pedunculata</i>	✓			
<i>Carex pensylvanica</i>	✓			
<i>Carex woodii</i>	✓			
<i>Caulophyllum thalictroides</i>	✓	✓		✓
<i>Claytonia virginica</i>	✓	✓	✓	
<i>Erythronium americanum</i>	✓	✓	✓	
<i>Geranium maculatum</i>	✓			
<i>Hydrophyllum virginianum</i>	✓	✓		
<i>Maianthemum canadense</i>	✓			✓
<i>Maianthemum racemosum</i>	✓			✓
<i>Mitella diphylla</i>	✓	✓		
<i>Osmorhiza claytoni</i>	✓			✓
<i>Podophyllum peltatum</i>	✓	✓		✓
<i>Polygonatum pubescens</i>	✓			
<i>Ranunculus abortivus</i>	✓			
<i>Sanguinaria canadensis</i>	✓	✓		
<i>Symplocarpus foetidus</i>	✓	✓		
<i>Tiarella cordifolia</i>	✓			
<i>Trillium erectum</i>	✓	✓		✓
<i>Trillium grandiflora</i>	✓	✓		✓
<i>Uvularia sessilifolia</i>	✓	✓	✓	
<i>Viola blanda</i>	✓	✓		
<i>Viola canadensis</i>	✓	✓		
<i>Viola conspersa</i>	✓	✓		
<i>Viola macloskeyi</i>	✓	✓		
<i>Viola pedata</i>	✓	✓		
<i>Viola pubescens</i>	✓	✓		
<i>Viola sororia</i>	✓	✓		

^a Collins and Pickett, 1987; Bratton, 1994; Bratton and Meier, 1998; McLachlan and Bazely, 2001; Small and McCarthy, 2002a.

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