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Responses of ground flora to a gradient of harvest intensity in the Missouri Ozarks

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Abstract

The relationship between the intensity of timber harvest and the composition and diversity of ground vegetation was investigated in upland mixed oak forests in the Missouri Ozarks. Pre- and post-harvest data were collected from 420 permanent vegetation plots to determine if changes in the composition and diversity of ground flora depended upon the intensity of the harvest treatment and, if so, how this varied among life forms of ground flora. The five harvest treatments (no-harvest control, single-tree selection, group selection, thinning, and clearcut) imposed a gradient of overstory canopy cover with reductions ranging from 12.8% in the controls to 83.6% in clearcuts. Both total cover and species richness of the ground flora increased proportionally to harvest intensity. Harvest intensity also caused a proportional impact on the collective relative cover of seven identified life forms of ground flora: annuals/biennials, forbs, graminoids, legumes, woody vines, shrubs, and tree seedlings. The direction of this change was nearly identical for all harvest treatments, reflecting the consistent and proportional decrease in the relative cover of legumes, and increase in the relative cover of annuals/biennials, forbs, graminoids, and woody vines, following all harvest treatments. Closer inspection revealed that changes in relative cover, compared to levels in uncut stands, were observed at different levels (thresholds) of harvest intensity for different life forms, although almost all life forms showed significant differences between uncut and clearcut conditions. Managers may be able to use these differential thresholds of response to harvest intensity to develop silvicultural prescriptions specifically intended to increase or decrease the short-term abundance of certain life forms.

Keywords: Forest ecology; Forest management; Ground flora; Ground vegetation; Landscape management; Missouri flora; MOFEP; Ozark flora; Silviculture; Species richness

1. Introduction

Timber harvesting is one of the most common anthropogenic disturbances in forests with the potential to influence the composition and structure of tree layer and ground flora in a stand (e.g., Grime, 1979; Huston, 1979; Collins and Pickett, 1982) and to change regional species diversity and abundances (McMinn, 1992; Hughes and Fahey, 1991). The ground flora, which represents the majority of plant species in many forest communities (Thomas et al., 1999), is tightly coupled to disturbances (Roberts and Dong, 1993; Gilliam et al., 1995; Hammond et al., 1998). Changes in the tree layer often lead to changes in ground flora compositions and distributions (Bergstedt and Milberg, 2001), with direction and magnitude of these changes being a function of the type and intensity of the disturbance and the disturbance history of the forest (White, 1979; Halpern and Spies, 1995; Roberts and Gilliam, 1995). There is growing concern that timber harvesting may have deleterious effects on the long-term maintenance of species diversity and composition (Burton et al., 1992), particularly with increasing disturbance intensity (e.g., clearcut).

Studies from other areas indicate that the species richness and diversity of the herbaceous ground layer respond variably to timber harvests. In some cases, no differences between

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clearcuts and controls were found (Yorks and Dabydeen, 1999; Gilliam, 2002; Roberts, 2002). In many cases, there were more species present after clearcutting (Peet and Christensen, 1988; Jenkins and Parker, 1999; Roberts and Zhu, 2002), but sometimes often only after some lag time or at the expense of some life forms (e.g., forbs, graminoids, shrubs, trees, etc.; Halpern, 1989; Halpern and McKenzie, 2001; Bergstedt and Milberg, 2001). Timber harvesting may increase species diversity by lowering the dominance of a few species or by increasing environmental heterogeneity (Connell, 1978; Tilman and Pacala, 1993). Species richness can also decrease after clearcutting (e.g., Halpern and Spies, 1995; Meier et al., 1995; Elliott et al., 1997) and recovery of the ground flora after logging may require several decades (Metzger and Schultz, 1984; Duffy and Meier, 1992). The reduction of species richness has also been observed in selection cuts, partial cuts, and thinnings (Metzger and Schultz, 1984; Meier et al., 1995), but the results are not universal (e.g., Fredericksen et al., 1999; Jenkins and Parker, 1999).

Although timber harvesting disturbances may result in significant short- and long-term changes to the ground flora (Bormann and Likens, 1979), few studies have examined how and to what extent the ground flora responds to the entire disturbance intensity gradient that is inherent in different regeneration methods (Roberts and Gilliam, 1995; Hammond et al., 1998; Roberts and Zhu, 2002). Because the ability to predict changes in ecosystem attributes in response to timber harvest is a necessary prerequisite for forest management, potential impacts of alternative silvicultural approaches on multiple ecosystem components and processes, such as the rate and direction of vegetational change, need to be better understood. Oak-dominated forests of the Central Hardwood Region provide an excellent opportunity to link the magnitude and direction of ground flora changes to different silvicultural systems, because these forests can be managed with even-aged (using clearcut, seed tree, and shelterwood regeneration methods) and uneven-aged (using single-tree and group selection regeneration methods) systems (Johnson et al., 2002). This study is part of the larger Missouri Ozark Forest Ecosystem Project (MOFEP) that contrasts the effects of different silvicultural systems (even-age, uneven-age, and no-harvest management) commonly used by forest managers on the flora and fauna of upland oak ecosystems at the landscape (site) and stand scales (Brookshire et al., 1997). Because harvest operations take place at the stand-level, the current study investigates whether or not understory vegetation as a whole and ground flora life forms respond differentially to harvest intensity at this operational scale. We present changes in cover and diversity of woody and herbaceous ground vegetation and relative cover of life form groups in upland oak communities.

2. Methods

2.1. Study area

Study sites were located in the Ozark Highlands in southeastern Missouri (37°00′–37°12′N and 91°01′–91°13′W). The area is characterized by a humid continental climate, with hot, humid summers and cool winters. The mean annual temperature is 13.3 °C and average annual precipitation is 112 cm with the majority of rain falling in spring and summer (Chen et al., 2002). The study sites encompass upland landscape positions, ranging from 170 to 360 m in elevation, 0 to over 60% slope, and spanning all aspects. Dominant parent materials are hillslope sediments, loess, and residuum (Meinert et al., 1997). Most soils are highly weathered Ultisols and Alfisols with mesic soil temperature and humid soil water regimes (Soil Survey Staff, 1996).

About 73% of the landscape is in mature, relatively unfragmented and homogeneous mixed oak-hickory upland forests (Guyette and Dey, 1997). Logging has not occurred in any of the study sites for at least 40 years. White oak (*Quercus alba* L.), black oak (*Quercus velutina* Am.), and scarlet oak (*Quercus coccinea* Muench) each represented about 20% or more of the live basal area for each site and dominated the sites, followed by shortleaf pine (*Pinus echinata* Mill.), post oak (*Quercus stellata* Wang.), and hickories (*Carya* spp.).

Most stands were fully stocked prior to harvest with a mean basal area of 21.8 m^2/ha (range 1.6–34.4 m^2/ha) and a mean stocking of 87% (range 8–126%; after Gingrich, 1967). Large trees ($\geq$11 cm dbh) constituted one-third of all trees and 86% of the basal area. Most overstory trees ranged from 50 to 70 years old; trees older than 100 years occurred on all sites and a few trees were older than 140 years (Shifley et al., 2000).

3. Harvest treatments

Our study was conducted within the six partially harvested MOFEP sites. MOFEP sites were: (1) at least 240 ha in size; (2) contiguous tracts with minimal edge; (3) largely free from silvicultural manipulations for at least 40 years; (4) owned by the Missouri Department of Conservation; (5) located in the southeast Missouri Ozarks; (6) in close proximity to each other (Brookshire et al., 1997). Sites ranged in size from 312 to 514 ha and were divided into stands averaging ca. 5 ha in size. A randomized complete block design was used in which sites in each of three blocks were randomly designated to be managed as even-aged (EAM), uneven-aged (UAM), or no-harvest (NHM) management. Because this is a long-term experiment with multiple future harvest entries, not all stands located in EAM and UAM sites received a harvest treatment. Stands located within EAM sites are subject to either a no cutting treatment (control, 142 plots), a thinning treatment (36 plots), or a clearcut with reserves harvest treatment (24 plots). Stands within the UAM sites are subject to either a no cutting treatment (control, 94 plots), a single-tree selection harvest treatment (79 plots), or a group selection harvest treatment (45 plots). Stands in the three NHM sites are not cut and were not used in the current study.

The first commercial timber harvest was implemented from May to October 1996 with the final removal of non-merchantable stems finished in May 1997 (Brookshire et al., 1997). Both thinned stands and stands harvested by the selection methods had roughly a 25% reduction in both trees per unit area and basal area. The residual basal area of clearcut

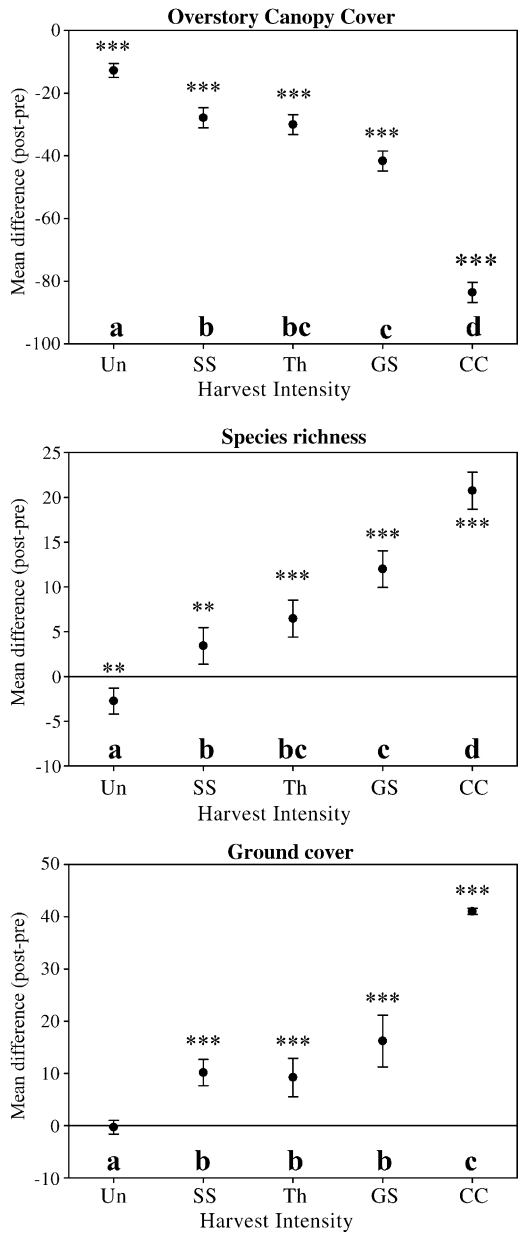

Fig. 1. Changes (least squares means) in percent of overstory canopy cover, mean species richness per plot and mean percent ground cover per plot of the ground layer for uncut (Un) stands, group selection (GS) and single-tree selection (SS) stands (UAM), and clearcut (CC) and thinned (Th) stands (EAM). Error bars are 95% confidence intervals. Asterisks indicate significant change following treatment (*<0.05, **<0.01, and ***<0.001). Differing letters indicate statistically significant group differences among treatments based on Tukey's H.S.D. multiple comparisons tests.

stands was 1.5 m^2/ha compared to 22 m^2/ha prior to harvest (Kabrick et al., 2002). Percent canopy cover was 82–85.9% prior to harvest and was reduced following treatment to 70.9, 57.4, 55.4, 40.3, and 2.3%, respectively, in uncut, single-tree selection, thinned, group selection, and clearcut stands (Fig. 1).

4. Ground vegetation inventory

Understory vegetation was sampled in one or two permanent 0.2 ha plots that were randomly placed within individual stands at each MOFEP site. Percent live foliar coverage of herbaceous and woody plants (including tree seedlings) <1 m tall was estimated in sixteen 1 m square quadrats that were placed 6 m at 45°, 135°, 225°, and 315° from the centers of four 0.02 ha subplots within each 0.2 ha plot. The density of woody vines, trees, and shrubs greater than 1 m tall but less than 3.8 cm dbh was sampled in the four 0.02 ha subplots. All live foliage within the quadrat was identified to species. Specific nomenclature follows that of Steyermark (1963). Pre-harvest data were collected during the summers of 1994 and 1995. Post-harvest data were collected in 1999 and 2000, 3–4 years following harvest treatments. Sites were sampled in the same order and during the same 2–3 weeks period each year to minimize potentially confounding seasonal effects. Post-harvest values for woody plant species greater than 1 m tall but less than 3.8 cm dbh were sampled during the winters of 1997/1998 and 2001/2002.

Plot-level species richness was the total number of species identified in each 0.2 ha plot. Plot-level percent ground cover was total cover averaged across the 16 quadrats in each plot. Each species was assigned to one of seven indigenous life form groups: (1) annual and biennial species; (2) non-leguminous forbs, herbaceous vines, and ferns; (3) graminoids (grasses, sedges, and rushes); (4) legumes; (5) woody vines; (6) shrubs; (7) tree seedlings. Relative cover was calculated as the ratio (times 100) of the sum of coverage for each life form group on each plot divided by the total sum of all life form coverages on that plot. Quadrats and subplots were combined to obtain mean plot-level estimates. Shannon–Wiener diversity (Greig-Smith, 1983), evenness/equitability (Pielou, 1977), and Simpson's dominance (McCune and Grace, 2002) were calculated by life form and then averaged to the plot-level (i.e., means across seven groups for each plot). Pre-harvest means were calculated as the average of 1994 and 1995 values, and post-harvest means were calculated as the average of 1999 and 2000 values.

4.1. Data analysis

For each site, we averaged stand-level responses of the ground flora by harvest intensity (i.e., clearcut, thinning, single-tree selection, group selection, and control). After no statistically significant differences were found for changes of any response variable among control stands (all p-values > 0.05), we combined control stands of EAM and UAM sites into one treatment type ('uncut').

Analysis of variance was used to test for pre-treatment differences in the response variables. ANOVA and analysis of covariance (in the case of significant pre-treatment differences, i.e., for relative cover of annuals/biennials) including pre-treatment level as an explanatory variable were used to test the hypothesis that vegetation changes were proportional to harvest intensity. When variances differed significantly among treatments (i.e., in the analysis of percent cover of ground flora and relative cover of legumes), a weighted least squares analysis was used. A weighted least squares analysis employing the inverse of the variance as weights is recommended to more closely follow the equal-variance assumption of ANOVA (see

Myers, 1990, p. 280). Tukey's HSD multiple comparison tests were used to investigate differences among harvest intensity treatments. Analyses were performed in SAS for Windows (version 8; SAS Institute, 1999). Nonmetric multidimensional scaling (NMS) using the Sørensen measure of similarity (in PC-ORD v. 4.27; McCune and Mefford, 1999) was used to evaluate the similarity in response to harvest intensities of the relative cover of the seven indigenous life forms. A low stress, two-dimensional solution found to have more structure than that expected by chance (based on a Monte Carlo procedure) captured 97% of the dataset variation.

5. Results

Ground flora across sites was diverse (gamma diversity >530 vascular species, 275 genera, and 85 families), but most species typically occurred in few plots and had low coverages (e.g., approximately 60% of all species were found on fewer than 10% of the plots). More than 80% of all species were native perennials; only 25 non-native species were identified, which were found in 11–14% of plots per treatment. Total numbers of species per site ranged from 309 to 381, with a mean of 356. Most species were found on two or more sites, with maximally 11 species unique to one site (Grabner et al., 1997).

Prior to treatment, average species richness per plot ranged from 34.6 to 53.5 and percent cover of ground flora from 20.5 to 22.9%. Tree seedlings were the most abundant life form prior to treatment, ranging from 36.4 to 45.3% cover, followed by legumes (21.8–28.8%), woody vines (5.9–18.9%), shrubs (8.9–12.5%), forbs (5.7–11.7%), and graminoids (0.9–3.5%), and annuals/biennials (0.1–0.5%). Statistically significant pre-treatment differences were observed only for annuals/biennials ($p = 0.007$), where uncut stands were significantly different from all other stands.

Following harvest, mean species richness significantly decreased in uncut stands and increased in all harvested stands, closely paralleling the gradient in harvest intensity (Fig. 1). Differences between clearcut and uncut stands were statistically significant and of substantial magnitude (e.g., differences of 24.2 species and 40.5% cover). Species richness and ground cover in clearcut stands were further significantly different from stands that were thinned or harvested by single-tree selection with and without group openings. Stands harvested with the selection methods responded intermediately between clearcut and uncut stands, but similarly to thinned stands. Species richness and ground cover increased more in stands with group selection openings than in single-tree selection openings.

There were significant differences in changes of Shannon diversity, evenness, and Simpson's dominance of life forms among harvest treatments (Table 1). In all cases, uncut, single-tree selection, and thinned stands changed similarly. Stands with group selection openings were statistically significantly different from uncut stands, but not from clearcut stands. With the greatest increase in life form diversity and evenness and the greatest decrease in dominance, clearcut stands were statistically significantly different from all stands except those with group selection openings.

Table 1
Change in Shannon diversity, evenness, and Simpson's dominance of the seven ground flora life forms following five harvest intensity treatments

	Uncut	Single-tree selection	Thinned	Group selection	Clearcut
Diversity	0.02 a	0.05 ab	0.06 ab	0.10 bc	0.15 c
Evenness	0.01 a	0.03 ab	0.03 ab	0.05 bc	0.08 c
Dominance	−0.02 a	−0.04 ab	−0.04 ab	−0.08 bc	−0.11 c

Numbers in rows followed by the same letters (a–c) are not significantly different at the $\alpha = 0.05$ level.

With the exception of a significant increase in relative cover of woody vines (Fig. 2), no relative cover changes of life forms were observed in uncut stands. In general, more changes and greater magnitudes of changes were observed in harvested stands and changes in relative cover of annuals/biennials, forbs, graminoids, legumes, and woody vines paralleled the gradient of harvest intensity. With the exception of legumes, relative cover of these life forms increased with harvest intensity. The pattern of change across all harvest treatments was weak and not significant for shrubs. Relative cover of tree seedlings decreased in all treatments, with significant decreases observed in group openings and clearcut stands.

The gradient in response of ground flora life forms to harvest intensity is clearly summarized in the NMS ordination diagram, which captured 91% of the variation on axis 1 and 6% on axis 2 (Fig. 3). The first axis corresponds almost perfectly to differences in pre-harvest versus post-harvest cover levels. The magnitude of these changes (as indicated by the lengths of the vectors from pre- to post-levels for each harvest treatment) is proportional to the intensity of harvest and increases from the uncut through to the clearcut treatment. Changes in the relative cover of life forms are seemingly parallel among harvest treatments, reflecting the substantial and consistent reduction in cover of legumes (axis 1, $r = -0.96$) and tree seedlings ($r = -0.84$) and an increase in relative cover for annuals ($r = 0.90$), woody vines ($r = 0.87$), and graminoids ($r = 0.95$) following all harvest treatments. Axis 2 correlated strongly with relative cover of forbs ($r = -0.87$) and moderately with that of woody vines ($r = 0.65$).

Closer inspection revealed that changes in cover were observed at different levels (thresholds) of harvest intensity for different life forms compared to uncut stands (Table 2; Fig. 2). Relative cover changes among harvest treatments for annuals/biennials, forbs, and graminoids were typically not statistically different from uncut stands for treatments with harvest intensities less than group selection openings. No differences were observed in changes of these life forms between stands harvested by single-tree selection and thinning treatments, between thinning and group selection openings, or between single-tree selection and group selection opening treatments. The lowest thresholds were found for legumes, for which single-tree selection and thinning treatments, respectively, already induced significant differences from uncut conditions. The clearcut treatment, however, induced significantly different

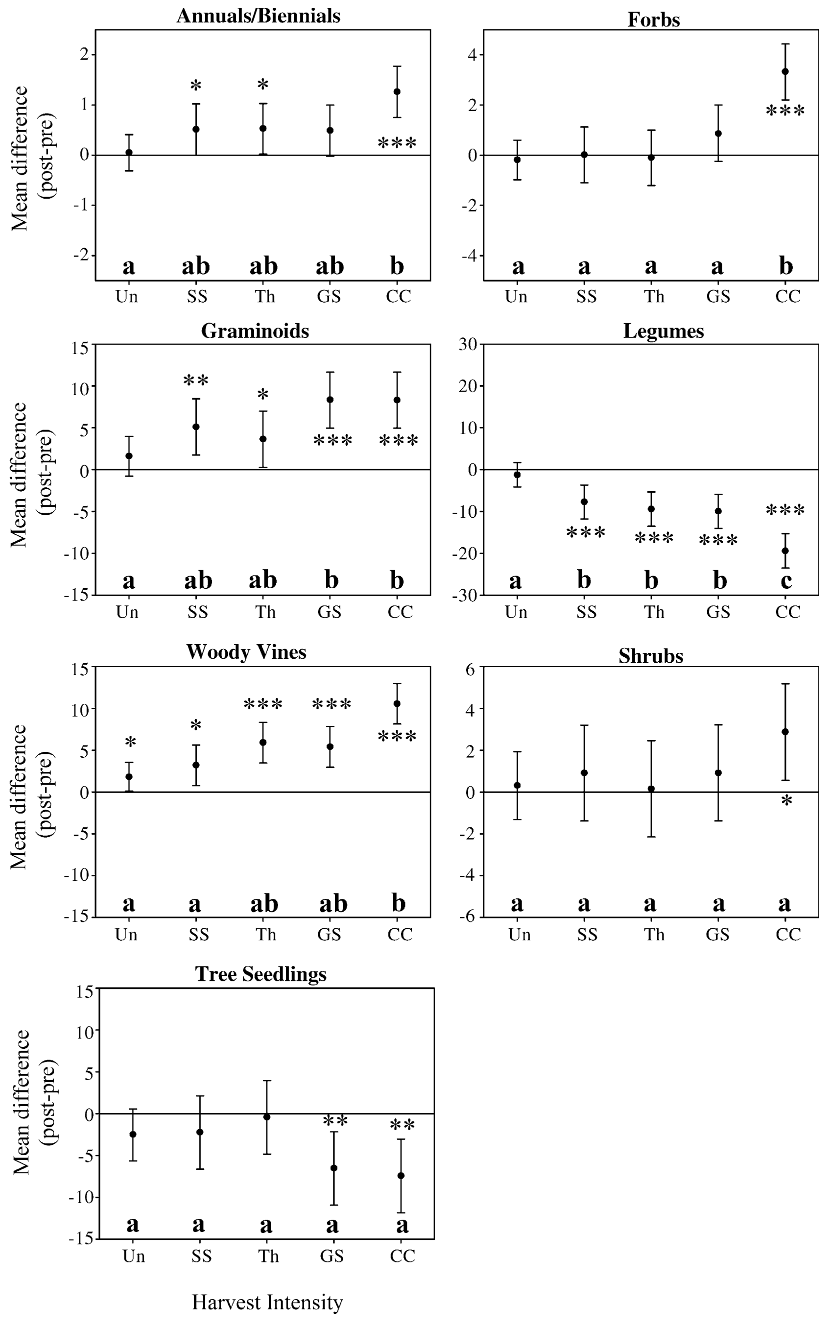

Fig. 2. Changes (least squares means) in relative cover of seven life form groups of the ground layer vegetation for uncut (Un) stands, group selection (GS) and single-tree selection (SS) stands (UAM), and clearcut (CC) and thinned (Th) stands (EAM). Error bars are 95% confidence intervals. Asterisks indicate significant change following treatment (*<0.05, **<0.01, and ***<0.001). Differing letters indicate statistically significant group differences among treatments based on Tukey's H.S.D. multiple comparisons tests.

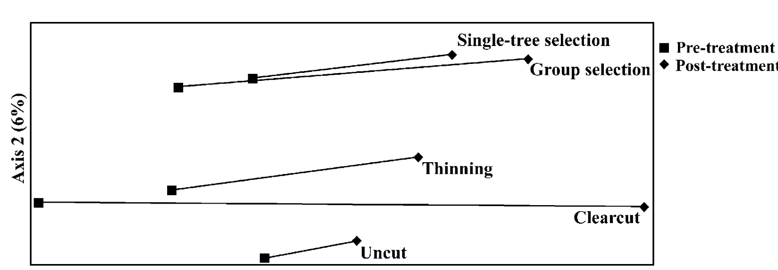

Fig. 3. The two-dimensional (unrotated) NMS ordination shows roughly parallel shifts in the relative cover of life forms from pre- to post-harvest conditions from left to right on axis 1, which captured 91% of the variation. The magnitude of this change, indicated by the length of the vectors, corresponds to harvest intensity.

Table 2
Pre- and post-harvest means of stem density per hectare of woody species greater than 1 m tall and less than 3.8 cm dbh

	Uncut	Single-tree selection	Thinned	Group selection	Clearcut
Woody vines					
1994/1995—pre	425 a	256 a	129 a	201 a	103 a
1997/1998—post	483 a	237 a	148 a	330 a	102 a
2001/2002—post	269 a	307 a	268 a	565 a	1533 b
Shrubs					
1994/1995—pre	358 a	212 ab	177 ab	60 b	6 b
1997/1998—post	356 a	299 a	296 a	219 a	14 b
2001/2002—post	191 a	360 ab	300 abc	485 bc	705 c
Trees					
1994/1995—pre	2180 a	1830 a	2088 a	1495 a	2171 a
1997/1998—post	2117 a	1432 a	1309 a	1745 a	3115 b
2001/2002—post	2320 a	3088 b	3062 ab	4592 c	16621 d

Numbers in rows followed by the same letters (a–d) are not significantly different at the $\alpha = 0.05$ level.

changes in relative cover from the uncut treatment for all life forms other than shrubs and tree seedlings.

Density changes of woody vines, shrubs, and trees in the stratum greater than 1 m tall and less than 3.8 cm dbh showed no relation to harvest intensity in 1997/1998 (Table 2; Fig. 4). By 2001/2002, these changes were strongly associated with harvest intensity. Clearcut, and to a lesser extent stands with group openings, showed particularly dramatic increases in density of trees, woody vines, and shrubs (Fig. 4). For example, by 2001/2002 tree density in clearcuts was over 7 times higher, in stands with group openings over 2 times higher, and in single-tree selection and thinned stands almost 1.5 times higher than in uncut stands (Table 2). Density of woody vines decreased slightly in uncut stands and increased significantly in clearcut and stands with group openings (Fig. 4), resulting in woody vine densities in clearcuts that were about seven times higher than in uncuts stands (Table 2). The density of shrubs decreased significantly in uncut stands, but increased significantly in clearcuts (Fig. 4), resulting in clearcut shrub densities that were nearly four times those observed in uncut stands (Table 2).

6. Discussion

The forests of MOFEP have undergone substantial change. The natural variability in these forests from year to year has been captured by changes observed in the uncut stands, which serve as controls for evaluating treatment effects, enabling us to observe a pattern of increased post-harvest species richness and cover in harvested stands that is consistent with other harvest impact studies. Not surprisingly, responses of life forms along the gradient of harvest intensity were variable, departing from uncut conditions at different levels of harvest intensity. This variability in thresholds of response could provide additional flexibility for MOFEP managers as they develop prescriptions to balance oak regeneration with biodiversity.

Pre- to post-harvest reductions in both canopy cover and species richness were observed in the uncut stands, reflecting a natural dynamic presumed to affect all of the MOFEP stands. Although we are unsure of the causes of the declines, a parallel decrease in the abundances of small mammals, reptiles, and amphibians was observed in the unharvested NHM sites (Kabrick et al., 2004). We find it likely that the widespread drought in southern Missouri throughout the late 1990s that may be responsible for these animal declines (Gram et al., 2003; Renken et al., 2004) could also be the cause for the reductions seen in this study. Presumably, the observed reductions also occurred in the harvested stands, but were overcome by treatment effects, perhaps with harvest reducing moisture stress in the upper soil layer by greatly reducing competition from overstory trees. Such responses would be in keeping with the findings of Fredericksen et al. (1999), who suggested that changes in understory composition in oak-hickory stands in Pennsylvania may be driven more by soil moisture and nutrients than by competition for light. In contrast, the natural decline in canopy cover in uncut stands appears to have produced a much less intense, but similar kind of disturbance, to that imposed by the harvest treatments. The changes in relative cover in uncut stands were typically in the same direction as the harvested stands, but of a lesser magnitude (Figs. 1 and 2). A similar conclusion was reached by Collins and Pickett (1988), who found that disturbances that co-occur with canopy openings may lessen or increase the response of the herb layer to the opened canopy.

The observed increases in ground cover and species richness in harvested stands, exceeding pre-harvest levels within 3–4 years, are consistent with previous research findings (e.g., Hannerz and Hånell, 1993; Quinby, 2000; Roberts and Zhu, 2002). Bergstedt and Milberg (2001) found logging intensity to have the highest explanatory power for ground cover vegetation change, in keeping with the findings of Fredericksen et al. (1999) that cover of forest floor vegetation increased with decreasing basal area. Jenkins and Parker (1999) found a similar trend to ours, where clearcuts and group-selection openings had significantly greater coverage of several species than single-tree selection openings and no-harvest control stands, which were often not significantly different from one another. Such increases have been attributed to increases in the relative availability of resources, especially light (Bormann and Likens, 1979; Gilliam et al., 1995), or to beneficial effects of

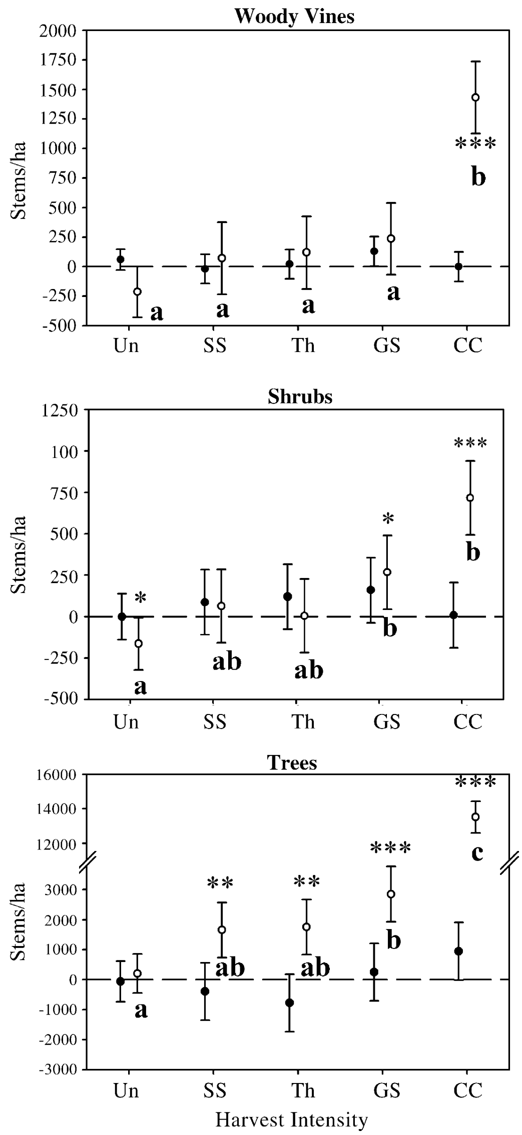

Fig. 4. Changes (least squares means) in stem density per hectare of three woody life form groups (woody vines, shrubs, and trees) greater than 1 m tall and less than 3.8 cm dbh for uncut (Un) stands, group selection (GS) and single-tree selection (SS) stands (UAM), and clearcut (CC) and thinned (Th) stands (EAM). Filled circles represent changes from 1994/1995 to 1997/1998. Open circles represent changes from 1997/1998 to 2001/2002. Error bars are 95% confidence intervals. Asterisks indicate significant change following treatment (*<0.05, **<0.01, and ***<0.001). Differing letters indicate statistically significant group differences among treatments based on Tukey's H.S.D. multiple comparisons tests. No statistically significant group differences were found for changes between 1994/1995 and 1997/1998 for any of the woody life forms.

slash (McInnis and Roberts, 1994) or soil disturbances (Dyrness, 1973; Halpern, 1989; Roberts and Gilliam, 1995), any of which may lead to the establishment of early-successional species. In this study, early-successional species of wood vines such as summer grape (*Vitis aestivalis* Michx.), blackberry (*Rubus pensylvanicus* Poir.), and Virginia creeper (*Parthenocissus quinquefolius* (L.) Planch.) strongly contributed to increases in ground cover following harvest. Although it is premature to argue that successional trajectories have been permanently altered, it is equally clear that these are not short-term impacts.

Taken as a whole, ground vegetation showed a clear response to harvest treatments, with relative species composition and abundance of life forms shifting in a parallel fashion from pre- to post-harvest levels with magnitudes commensurate to the harvest intensity. The relative magnitudes of these shifts show that the ground vegetation community as a whole demonstrated an unequivocal response to increased harvest intensity. The comparable direction of these shifts reflects the consistent reduction in the dominance of some life forms (legumes and tree seedlings) and increases in others (woody vines, graminoids, and annuals/biennials) along this harvest intensity gradient. The reduction in relative cover of tree seedlings, however, is a function of increased growth response, particularly in clearcuts and group openings. In these treatments, tree densities that grew into the next canopy stratum increased dramatically after 1997/1998. Densities of woody vines and shrubs over 1 m also increased with harvest intensity, but to a lesser extent than trees. Clearcuts and group selection openings had a more even distribution of life forms, resulting in a significantly larger reduction in Simpson's dominance and significantly larger increases in Shannon diversity and evenness than in uncut, single-tree selection, and thinned stands. It thus appears that timber harvesting can increase life form diversity by lowering the dominance of some species (Connell, 1978; Tilman and Pacala, 1993).

This impact, however, only appeared after a threshold of harvest intensity was reached. For example, among annuals/biennials, forbs, graminoids, and woody vines, there is little difference in response among the harvest treatments on the very low end of the harvest intensity gradient (uncut, single-tree selection, and thinning). A similar conclusion was reached by Bergstedt and Milberg (2001), who found that many understory species were indifferent to low and intermediate logging intensities and that a reduction of over 80% of standing timber was needed before some life forms responded to harvesting. In fact, even group openings did not induce significant changes in the relative cover (compared to uncut stands) of annuals/biennials, forbs, and woody vines in this study. Only in clearcut stands were differences to uncut stands consistently observed.

7. Management implications

Management objectives for Missouri's forests are very complex and include the maintenance of ecosystem processes, conservation and restoration of habitat for neotropical migrant songbird, small mammal, and herpetofaunal communities, creation of forests with old-growth attributes, and extraction of commodities (Missouri Department of Conservation, 1986). Because of the importance of ground flora in forest communities, changes in ground flora following forest harvesting have become an important consideration in forest management in recent times. Anticipated changes in the ground flora must also be balanced with the desire to perpetuate mixed oak forests through regeneration. Mixed oak stands have been successfully regenerated using various regeneration methods ranging from clearcuts to single-tree selection (Johnson et al., 2002), giving managers great flexibility in harvest intensity.

This paper shows that there are different impacts on the ground flora life forms depending on the methods of forest management employed in the Missouri Ozarks. The observed variability in the responses of individual life forms provides assistance to managers wishing either to maintain a balance of different life forms or to enhance some life forms and thereby plant community structure without diminishing others. The fact that different life forms respond to harvest at different intensities indicates that managers will have greater flexibility in the harvest methods they employ as long as the threshold level for a given life form is not exceeded. In these stands, it appears that for many life forms this includes harvest intensities up to, and in some cases including, group selection openings.

Acknowledgments

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