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Effects of harvesting on herbaceous layer diversity of a central Appalachian hardwood forest in West Virginia, USA

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Abstract

Clearcutting is a common harvesting practice in many eastern hardwood forests. Among the vegetation strata of these forests, the herbaceous layer is potentially the most sensitive in its response to harvest-mediated disturbances and has the highest species diversity. Thus, it is important to understand the response of herbaceous layer diversity to forest harvesting. Previous work on clearcut and mature stands at the Fernow Experimental Forest (FEF), West Virginia, has shown that, although, harvesting did not alter appreciably herbaceous layer cover, it influenced the relationship of cover to biotic and abiotic factors, such as tree density and soil nutrients, respectively. The purpose of this study was to examine the response of species diversity of the herbaceous layer to harvesting at FEF. Fifteen circular, 0.04 ha sample plots were established in each of four watersheds (60 plots in total) representing two stand age categories: two watersheds with 20 years even-age stands following clearcutting and two watersheds with mature second growth stands. All woody stems $\geq$2.5 cm diameter at breast height were identified, tallied, and measured for diameter. The herbaceous layer was sampled by identifying all vascular plants $\leq$1 m in height and estimating cover for each species in each of 10 (1 m^2) circular sub-plots per sample plot (600 sub-plots total). Species diversity for each plot was calculated from herbaceous layer data using the ln-based Shannon Index (H') equation. Ten stand and soil variables also were measured on each plot. Mean herbaceous layer cover for clearcut versus mature stands was $27.2 \pm 14.3\%$ versus $20.2 \pm 8.1\%$ ($P > 0.05$), respectively and mean H' was 1.67 ± 0.42 versus 1.55 ± 0.48 ($P > 0.05$), respectively. Herbaceous layer diversity was negatively correlated with cation exchange capacity and extractable Ca and Mg in the mineral soil in clearcut stands. In contrast, herbaceous layer diversity was positively correlated with soil organic matter and clay content. Although, 20 years of recovery after clearcutting did not have significant effects on the species diversity of the herbaceous layer when examining stand age means alone, harvesting did appear to influence the spatial relationships between herbaceous layer diversity and biotic factors (e.g. tree density) and abiotic factors (e.g. soil nutrients). © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Herbaceous stratum; Eastern deciduous forest; Disturbance effects; Shannon–Wiener index

1. Introduction

In response to the acceleration in species-loss at a global scale (Ehrlich and Wilson, 1991), resource management policies in recent years have shifted their focus to the level of the ecosystem, emphasizing the potential contribution and importance of all species, not just those that are of immediate commercial value. For management of forest resources, this suggests that the goals of management should be not only to maintain natural diversity and species composition to the extent possible, but also to enhance diversity of native species where anthropogenic activity has caused its decline (Roberts and Gilliam, 1995a). Such an approach can be challenging in considering the

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effects of harvesting on the herbaceous stratum of forest stands, especially in some forests of the eastern US with their extremely high non-tree species richness (Ricketts et al., 1999). Furthermore, the low dispersal rates expected for most forest herbaceous species (Cain et al., 1998) may limit their ability to re-colonize an area disturbed by intense harvesting.

The herbaceous layer plays an important role in the highly stratified hardwood forests of the region. For example, it is the stratum of initial competition among herbaceous species and seedling/sprouting individuals of potential over-story dominants, a competitive response that can be highly species-specific among tree species (Maguire and Forman, 1983; George and Bazzaz, 1999a,b). The herbaceous layer is also potentially quite sensitive to soil fertility and site conditions (Siccama et al., 1970; Peterson and Rolfe, 1982). Consequently, the herbaceous layer has been used as an indicator of general edaphic factors and forest site quality (Pregitzer and Barnes, 1982; Strong et al., 1991; Host and Pregitzer, 1992; Barnes et al., 1998; Dibble et al., 1999).

Plant species of the herbaceous layer can respond to a range of forest disturbances, ranging from micro-disturbances, such as frost heaving and trampling by large vertebrates (McCarthy and Facelli, 1990), to more intensive disturbances related to tree mortality (Beatty, 1984; Moore and Vankat, 1986; Peterson et al., 1990; Stone and Wolfe, 1996; Goldblum, 1997), flood (Lyon and Sagers, 1998), fire (Gilliam and Christensen, 1986; De Granpré and Bergeron, 1997), and forest management practices (Duffy and Meier, 1992; Roberts and Dong, 1993; Hammond et al., 1998; Wender et al., 1999). Indeed, forest management systems commonly used throughout the eastern deciduous forest (except for plantations) represent a gradient of disturbance intensity, from the least intense with single tree selection to the most intense with clearcutting (Gilliam and Roberts, 1995; Hammond et al., 1998).

Several recent studies have examined the direct effects of harvesting, alone and in combination with other management techniques, on herbaceous layer composition and diversity (Halpern and Spies, 1995; Roberts and Gilliam, 1995b; Elliott et al., 1997; Hammond et al., 1998; Wender et al., 1999). Other work has studied the recovery of herbaceous species following such extreme treatments as deforestation and re-growth suppression with herbicide treatments (Kochenderfer and Wendel, 1983; Reiners, 1992). Still others have provided valuable information on species dynamics of the herbaceous layer by comparing patterns in second-growth to those in old-growth forest stands (Qian et al., 1997; Goebel et al., 1996). The lack of consistency in findings of these studies demonstrates the site-specific nature of herb-layer responses to anthropogenic disturbances to forests (Roberts and Gilliam, 1995b), precluding broad generalizations and underlining the importance of in-depth study of these responses for different forest types and harvest techniques.

Most work carried out on experimental watersheds of the Fernow Experimental Forest (FEF) in north-central West Virginia has focused on hydrologic and nutrient cycling (e.g. Adams et al., 1993, 1994; Gilliam et al., 1994, 1996; Gilliam and Adams, 1996; Adams et al., 1997). Other works examined responses of over-story and herbaceous layer species to forest cutting. Studies comparing two watersheds supporting 20-year-old, even-age stands with two watersheds that support mature, mixed-age stands have shown a surprisingly high degree of similarity in species composition of both strata among stands of contrasting age (Gilliam and Turrill, 1993; Gilliam et al., 1995).

Gilliam and Turrill (1993) examined patterns of herbaceous layer cover for one watershed from each of the two stand ages. They concluded that although harvesting did not alter appreciably herbaceous layer cover, it influenced the relationship of cover to biotic and abiotic factors (e.g. tree density and soil nutrients, respectively). Gilliam et al. (1995) focused on the effects of harvesting on species composition of the over-story and herbaceous layer, and on interactions between the two strata. They found few differences in species composition of the herbaceous layer related to stand age, in contrast to that of the over-story, which was dominated by shade-intolerant species in young stands and by shade-tolerant species in mature stands. Neither of these studies, however, provided a quantitative assessment of the effects of harvesting on herbaceous layer diversity.

The purpose of the present study was to provide a focus on the species diversity of the herbaceous layer of clearcut and mature central Appalachian hardwood stands. Specifically, the following questions were addressed: (1) what are the responses of herbaceous layer diversity to clearcutting? (2) what biotic and abiotic factors can be important in influencing herbaceous layer diversity? and (3) how might relationships between herbaceous layer diversity and these factors vary as a result of clearcutting?

2. Materials and methods

2.1. Study site

This study was part of on-going research in the ecology and dynamics of central Appalachian hardwood forests at the FEF. The FEF is a ~1900 ha area of largely montane hardwood forest in the Allegheny mountain section of the unglaciated Allegheny plateau, Tucker County, West Virginia, USA. Mean annual precipitation is approximately 143 cm per year, most of which occurs during the growing season (Gilliam and Adams, 1996). Four contiguous watersheds were selected for this study: WS7 and WS3 were ~20-year-old, even-aged stands following clearcutting (hereafter ‘clearcut’ stands), and WS13 and WS4 were uneven-aged stands (>70-year-old, hereafter ‘mature’ stands). WS7 and WS3 differ in stand history, as WS7 was cut between 1963 and 1967 and treated with herbicide to eliminate re-growth until late 1969, WS3 was clearcut to a DBH limit of 2.5 cm in 1970.

The study watersheds support primarily mixed hardwood stands. Most tree species occur in both clearcut and mature stands, although species dominance varies greatly with stand age. Dominant tree species on FEF watersheds are black birch (*Betula leuta* L.), black cherry (*Prunus serotina* Ehrh.), yellow poplar (*Liriodendron tulipifera* L.) (clearcut stands) and sugar maple (*Acer saccharum* Marshall) and northern red oak (*Quercus rubra* L.) (mature). The herbaceous layer is heterogeneous along elevation gradients in all stands, but the herbaceous layer species vary less with stand age than do over-story species. Dominant herbaceous layer species are stinging nettle (*Laportea canadensis* (L.) Wedd.), violets (*Viola* spp.), and several ferns. Nomenclature follows Gleason and Cronquist (1991). Some of the more important herbaceous layer species from both age classes are given in Table 1.

Soils are similar among study watersheds. These are relatively thin (<1 m in depth), acidic, sandy-loam Inceptisols of two series: (1) Berks (loamy-skeletal, mixed, mesic typic dystrochrept) and (2) Calvin (loamy-skeletal, mixed, mesic typic dystrochrept) (Gilliam et al., 1994). Further details of all four study watersheds can be found in Gilliam et al. (1995).

Table 1
Important herbaceous layer (vascular plants $\leq$1 m tall) species of young vs. mature stands of Fernow Experimental Forest, WV[a]

Species	Stand age class	
	Young[b]	Mature[c]
Acer pensylvanicum L.	7.4	17.3
Dryopteris marginalis (L.) A. Gray	29.5	5.8
L. canadensis (L.) Wedd.	17.0	27.4
Polygonatum biflorum (Water) Elliott	–	10.2
Polystichum acrostichoides (Michx.) Schott	8.6	14.8
Prunus serotina Ehrh.	9.1	4.7
Rubus spp.	11.7	3.9
Sassafras albidum (Natt.) Nees	7.9	–
Smilax rotundifolia L.	14.4	8.9
Viola spp.	19.6	20.1

[a] Data are mean importance values (sum of relative cover and relative frequency) for two watersheds per age class. Nomenclature follows Gleason and Cronquist (1991).

[b] ~20 years. (WS7, WS3).

[c] >70 years. (WS13, WS4).

2.2. Field sampling

Data for over-story and herbaceous layer species were collected in the summer of 1991 and have been reported for each watershed separately (Gilliam et al., 1995). Fifteen circular 0.04 ha sample plots were established in each watershed for a total of 30 plots for each of the clearcut and mature stands. In each plot, all woody stems $\geq$2.5 cm diameter at ~1.3 m in height (DBH) were tallied, identified and measured for DBH to the nearest 0.1 cm. The herbaceous layer was sampled by identifying and estimating the cover of all vascular plants $\leq$1 m in height within 10 (1 m^2) circular sub-plots in each sample plot, using a visual estimation method as described in Gilliam and Turrill (1993), for a total of 300 sub-plots sampled for each stand age. Sub-plots were located within sample plots using the stratified-random polar coordinates method of Gaiser (1951). Because only minor differences were found between the two watersheds within each stand age class, and because the focus of this paper

Table 2
Soil variables of clearcut vs. mature stands at the Fernow Experimental Forest, WV. OM: organic matter; N: sum of extractable NO_3 and NH_4[a]

Stand	OM (%)	pH	CEC (meq/kg)	N (μeq/g)	P (μeq/g)	Ca (μeq/g)	Mg (μeq/g)	K (μeq/g)
Clearcut	13.8 ± 0.7	4.39 ± 0.06	45.5 ± 4.6	3.3 ± 0.2	0.8 ± 0.4	12.6 ± 5.0	2.1 ± 0.4	2.3 ± 0.2
P	<0.1627	<0.4169	<0.2640	<0.1090	<0.3560	<0.2342	<0.7086	<0.7380
Mature	12.6 ± 0.4	4.32 ± 0.05	40.1 ± 1.2	2.8 ± 0.2	0.4 ± 0.0	6.4 ± 1.1	2.4 ± 0.7	2.2 ± 0.1

[a] Values expressed are mean ± 1S.E.; significance of difference between stand ages determined with a *t*-test (Zar, 1996). Data taken in part from Gilliam and Adams (1995).

is on stand age-related comparisons, these data are combined here into two stand age/treatment classes: (1) clearcut; and (2) mature.

Methods for sampling mineral soil were described in Gilliam et al. (1994) and Gilliam and Adams (1995). Briefly, two 10 cm deep samples were taken from each plot and placed into separate bags, thus, values for each plot represented means of two soil samples. Each sample was sieved with a 2 mm screen, air-dried, and analyzed for (1) pH as a 1:1 (weight: volume) soil:water slurry, (2) 1N KCl-extractable Ca, K, Mg and P with inductively-coupled plasma emission spectrophotometry, (3) 1N KCl-extractable NO_3 and NH_4 with flow-injection colorimetry, and (4) organic matter with a loss-on-ignition method. Particle size (texture) was determined for each soil sample using the hydrometer method.

2.3. Data analysis

Means for soil variables and over-story structure (Tables 2 and 3) and measures of herbaceous layer species richness/diversity were compared between stand ages with *t*-tests (Zar, 1996). Species richness was assessed for each stand age based on plot values representing two spatial scales. The first was that of the sample plot, wherein richness was measured as all species encountered in all 10 (1 m^2) sub-plots per sample plot (S_p) (i.e. the number of herbaceous layer species expected to be found in a sample plot). The second was that of the sub-plot, wherein richness for each sample plot was expressed as a mean of individual subplot richness (S_{sp}) (i.e. the number of herbaceous layer species expected to be found in a 1 m^2 sub-plot).

Scale-dependent distinctions in measurements of species richness were made in this paper because the response of herbaceous layer species to environmental factors can be sensitive to processes that vary with and are dependent on spatial scale. For example, richness at the 1 m^2 sub-plot scale should suggest herbaceous layer responses to variation in micro-climate that might result, from differences in micro-topography (Beatty, 1984). Richness at the 400 m^2 plot scale should suggest responses to larger scale variation, such as canopy gap formation (Collins et al., 1985). Consequently, what is found as stand age-related differences in richness at one scale might not be found at another. Both scales, however, are important in considering herbaceous layer responses to disturbance.

Species diversity of the herbaceous layer was calculated on a per plot basis using the ln-based Shannon index (H') equation (Magurran, 1988). The

Table 3
Over-story structural and herbaceous layer cover and diversity measures in clearcut vs. mature stands[a]

Stand	Basal area (m^2/ha)	Density (stems/ha)	Herb cover (%)	S_p (species/plot)	S_{sp} (species/m^2)	Diversity (H')	Evenness (J')
Clearcut	21.3 ± 0.9	2098 ± 95	28.4 ± 2.8	13.9 ± 0.7	4.3 ± 0.2	1.64 ± 0.08	0.63 ± 0.03
P	<0.00001	<0.00001	<0.1013	<0.4275	<0.0780	<0.3633	<0.4393
Mature	35.9 ± 1.9	854 ± 46	22.2 ± 2.5	13.2 ± 0.5	3.8 ± 0.2	1.53 ± 0.08	0.59 ± 0.03

[a] S_p is species richness for the herbaceous layer on a plot basis; S_{sp} is species richness for the herbaceous layer on a sub-plot basis (see Section 2). Values expressed are mean ± 1 S.E.; significance of difference between stand ages determined with a *t*-test (Zar, 1996).

utility of such indices of species diversity as the Shannon index is that they provide a way to combine the number of species in a community (richness) with a quantitative expression of how evenly dominance or importance is distributed among those species (evenness) (Magurran, 1988; Barbour et al., 1999). Because H' combines both species richness and evenness, richness and evenness can have varying influence on H'. Accordingly, the Pielou's evenness index (J') was also determined for each plot (Pielou, 1966). Relationships between H' and richness (S_p) and between H' and evenness were determined with linear regression (Zar, 1996). Because these relationships did not vary significantly between stand ages (data not shown), data for all 60 plots were combined for this analysis, and mean H' was determined for each richness level. Similarly, mean H' was determined for each evenness level after J' values were rounded to the nearest 0.05.

Relationships between richness/diversity measures (S_p, S_{sp}, and H') and environmental data were determined with Pearson product–moment correlation (Zar, 1996). Differences between means of variables for both stand ages were assumed to be significant at $P < 0.05$. Correlations between measured variables also were assumed to be significant at $P < 0.05$.

The statistical design of this study is an example of simple pseudo-replication, a common characteristic of ecosystem studies at the watershed scale (Hurlbert, 1984), thus, our data should be interpreted with that in mind. It is a reasonable contention, however, that the effects reported here are treatment effects, rather than pre-existing differences among watersheds, given the close similarities among watersheds in several 'site' variables such as soil texture and fertility (Gilliam and Adams, 1995).

3. Results

None of the soil variables was significantly different in clearcut versus mature stands at $P < 0.05$ (Table 2). By contrast, both over-story structural variables (tree basal area and stem density) varied significantly ($P < 0.00001$) between clearcut and mature stands. Total tree basal area was approximately 70% higher in mature stands than in clearcut stands, whereas stem density was nearly 150% higher in clearcut stands than in mature stands (Table 3). None of the measured characteristics of the herbaceous layer, including total herb cover, S_p, S_{sp}, H', and J', was significantly different between clearcut and mature stands at $P < 0.05$ (Table 3).

Linear relationships were significant between mean herbaceous layer species diversity and both species richness (S_p) ($P < 0.00001$) and species evenness ($P < 0.00001$), with r^2 values of 0.51 and 0.97, respectively (Figs. 1 and 2). Herbaceous layer species richness on a plot basis (S_p) was positively correlated

Table 4
Correlation between richness/diversity measures of the herbaceous stratum and environmental factors at Fernow Experimental Forest[a]

Factor	S_p		S_{sp}		H'	
	Clearcut	Mature	Clearcut	Mature	Clearcut	Mature
Elevation	0.09	−0.23	−0.09	−0.22	−0.10	0.29
Basal area	$-\underline{0.39}$	0.12	$-\underline{0.46}$	0.24	−0.25	0.22
Tree density	$-\underline{0.43}$	−0.33	$-\underline{0.54}$	$-\underline{0.37}$	−0.01	0.21
Herb cover	$\underline{0.49}$	0.08	$\underline{0.42}$	0.15	−0.25	0.07
Clay content	$-\underline{0.60}$	−0.33	$-\underline{0.57}$	$-\underline{0.44}$	−0.16	$\underline{0.40}$
OM	−0.01	0.07	−0.06	−0.01	−0.17	$\underline{0.42}$
CEC	−0.20	−0.01	−0.31	−0.12	$-\underline{0.39}$	0.16
pH	0.26	$\underline{0.50}$	0.24	$\underline{0.47}$	−0.26	−0.18
N	−0.16	0.15	−0.11	0.03	−0.17	0.33
P	0.21	−0.07	0.06	0.12	−0.04	0.26
Ca	−0.10	0.30	−0.20	0.24	$-\underline{0.39}$	0.01
Mg	−0.10	0.14	−0.21	0.11	$-\underline{0.37}$	−0.09
K	0.16	$\underline{0.38}$	0.15	0.31	−0.11	0.07

[a] Abbreviations and units used for all variables are as those given in Tables 2 and 3. Values shown are Pearson product–moment correlation coefficients (Zar, 1996). An underline indicates a significant correlation at $P < 0.05$.

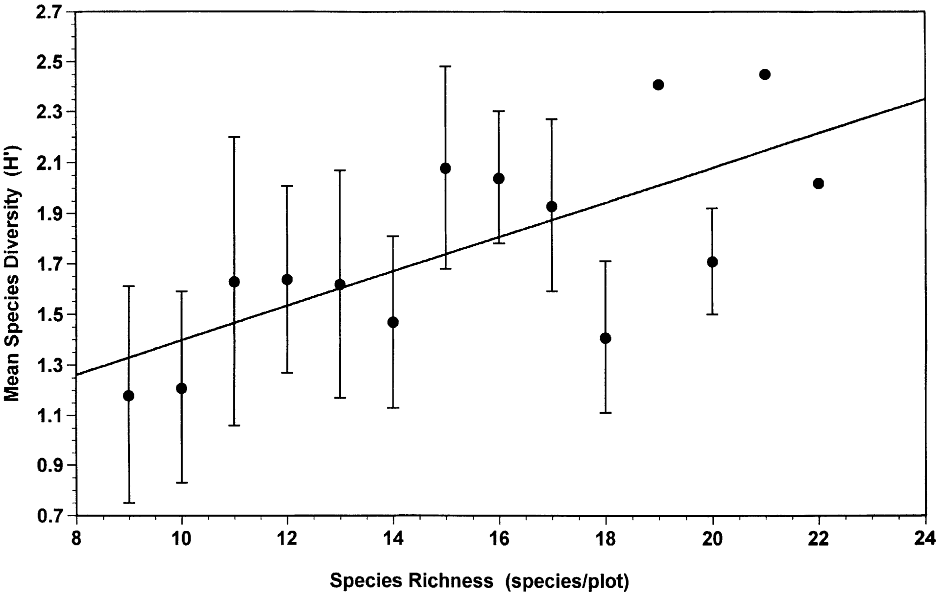

Fig. 1. Linear regression between Shannon index (H') and species richness (S_p: number of species per plot) for the herbaceous layer at Fernow Experimental Forest. Data are combined for clearcut and mature stands. Values shown are mean H' per richness level; error bars are ±1 standard deviation of the mean. Points without error bars represent a richness level where $n = 1$. Equation for line shown is: $H' = 0.72 + 0.07S_p$; $r^2 = 0.51$; $P < 0.00001$.

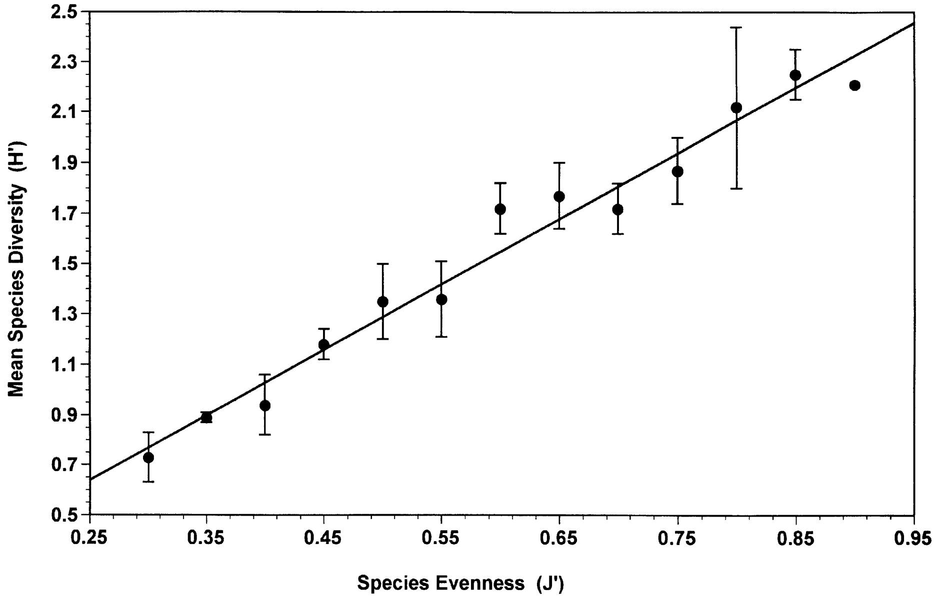

Fig. 2. Linear regression between Shannon index (H') and Pielou's evenness index (J') for the herbaceous layer at Fernow Experimental Forest. Data are combined for clearcut and mature stands. Values shown are mean H' per evenness level; error bars are ±1 standard deviation of the mean. Points without error bars represent a evenness level where $n = 1$. Equation for line shown is: $H' = -1.04 + 2.60J'$; $r^2 = 0.97$; $P < 0.00001$.

($P < 0.05$) with herb cover, and negatively correlated with tree basal area, stem density, and clay content in clearcut stands (Table 4). S_p was positively correlated with pH and K, and negatively correlated with stem density and clay content in mature stands. Patterns of significant correlations for S_{sp} were similar to those for S_p in both clearcut and mature stands. H' exhibited only negative correlations with environmental factors in clearcut stands, including cation exchange capacity (CEC) and extractable Ca and Mg. By contrast, H' exhibited only positive correlations with environmental factors in mature stands, including clay content and organic matter (Table 4).

4. Discussion

The lack of significant differences between clearcut and mature stands for soil variables (Table 2) strongly suggests that harvesting had either no effect on soils or the effect was small enough to allow recovery of organic matter, pH, cation exchange capacity, and extractable nutrients to pre-harvest conditions in a 20-year period. Similarities between clearcut and mature stands emphasize the general similarities of watersheds of the FEF, and this supports earlier conclusions by Gilliam et al. (1994) and Gilliam and Adams (1995).

In contrast to lack of differences between stand ages for soil variables, differences between stands for the two stand structural variables (tree basal area and stem density) were highly significant ($P < 0.00001$, Table 3). Basal area for the mature stands was nearly twice that of the basal area for the young stands. Conversely, stem density for the young stands was nearly 2.5-times that for the mature stands. Such differences are typical of competitive thinning that occurs during secondary forest succession (Yoda et al., 1963; Christensen and Peet, 1984; Roberts and Richardson, 1985). Hardt and Swank (1997) found similar age-related differences in stand structural variables in young versus mature southern Appalachian mixed hardwood forests.

4.1. Effects of harvesting on herbaceous layer richness and diversity

Although Magurran (1988) considered the Shannon index to be influenced more by richness than by evenness, theoretically the influence of richness and evenness on diversity may vary in importance (e.g. high diversity can arise from moderate evenness with high richness, or from moderate richness with high evenness). Species diversity, measured as the Shannon index (H'), of the herbaceous layer in clearcut and mature stands at FEF is clearly influenced more by species evenness, measured as the Pielou's index (J'—Pielou, 1966), than by richness, measured as the number of species encountered in a plot (S_p) (Figs. 1 and 2). Coefficients of linear regressions (r^2) for diversity/richness and diversity/evenness were 0.51 and 0.97, respectively, i.e. whereas variation in richness explained only one-half of the variation in species diversity, variation in evenness explained nearly all of the variation in diversity. Neither H' nor J' varied significantly between clearcut and mature stands (Table 3).

Mean plot richness (S_p) was similar for clearcut and mature stands at 13–14 species per sample plot (Table 3). In fact, the range of S_p values was virtually identical, 9–22 species per plot for the clearcut stands and 9–20 species per plot for the mature stands. As with S_p, the range of S_{sp} values were similar between stands 2–7 species/m^2 in clearcut stand plots and 2–6 species/m^2 for mature stand plots.

Following the ~20-years of recovery, clearcutting with subsequent treatment appears to have had minimal effects on species diversity of the herbaceous layer of this central Appalachian hardwood forest, regardless of which diversity measure is used. This is not to suggest that clearcutting does not influence herbaceous layer species. Hammond et al. (1998), for example, found that clearcutting in mixed-oak forests of Virginia caused more change in species than did other harvest techniques such as group selection and shelterwood harvesting. Rather, these results suggest that herbaceous layer recovery can be as short a period as 20-years at FEF. Kochenderfer and Wendel (1983) reported dramatic changes in composition and dominance of herbaceous layer species during the first 10-years of recovery for WS7 (one the two clearcut watersheds in this study). They reported immediate dominance of the disturbance-maintained fireweed (*Erichtites hieracifolia* (L.) Raf.) (~40% of total plant cover) that virtually disappeared by the following year. Blackberries (*Rubus* spp.), which are also largely disturbance-maintained species (Roberts and Dong, 1993), increased from ~20% of plant cover in year 1 to nearly 40% by year 5 and then declined rapidly by year 10 (Kochenderfer and Wendel, 1983). Reiners (1992) reported a similar pattern of dynamic change in species dominance over a 20-year period of recovery at Hubbard Brook Experimental Forest.

Several recent studies have looked at post-harvest responses of herbaceous layer vegetation to clearcut harvests either alone or in combination with other silvicultural treatments. These studies have reported findings comparable to those presented here. Halpern and Spies (1995) found that changes in herbaceous layer diversity were short-lived following clearcutting and slash burning of Douglas-fir forests of western Oregon and Washington, and that herb diversity returned to pre-harvest conditions before canopy closure (10–20 years). Roberts and Gilliam (1995b) found that responses of the herbaceous layer to clearcutting were highly site-dependent in mesic and dry-mesic aspen stands. Harvested stands ~15-year-old had higher diversity and richness than mature stands on mesic sites, whereas there were no significant differences on dry-mesic sites. De Granpré and Bergeron (1997) found that site-dependence of herb response to disturbance might be related to the age of the stand at the time of disturbance in southern boreal forest of Québec, i.e. younger communities changed less following clearcutting than did more mature communities. Fredericksen et al. (1999) concluded that only the most intensive levels of harvesting measurably affected herbaceous layer richness, diversity, composition and cover in northern hardwood and oak-hickory forests of Pennsylvania.

An additional explanation should be considered when evaluating results of the present study and those of other studies that conclude that harvesting had minimal effects on the herbaceous stratum. It is possible that the more commonly used indices of richness and diversity do not adequately capture all of the more subtle changes that can occur, such as loss of rare, infrequent species. However, a complete floristic study by Aulick (1993) of three of the study watersheds (WS3, WS4, WS7) found data to suggest that such losses were minimal at FEF.

4.2. Factors influencing herbaceous layer richness and diversity

Although clearcutting did not have long-term impacts on richness and diversity of the herbaceous layer, richness and diversity differed in relationships to over-story and soil factors that could be related to clearcutting. Richness (both S_p and S_{sp}) was negatively correlated with basal area and tree density ($P < 0.05$) and positively correlated with herbaceous layer cover ($P < 0.05$), indicating that availability of light might determine establishment of new species in the recovering clearcut stands. That is, higher herb cover in the clearcut stands occurred from the addition of more species, rather than from increased growth of a few species. These significant correlations were generally not found for mature stands (Table 4).

It is important to note that correlations of H' with over-story and soil factors differed from those of richness with over-story and soil factors (Table 4). For example, H' correlated with neither basal area nor density for both clearcut and mature stands. Correlations of H' with soil factors varied substantially between stand types. Significant correlations for herbaceous layer H' in clearcut plots were all negative and were generally associated with soil exchangeable factors, including CEC and extractable Ca and Mg. Availability (i.e. extractability) of Ca and Mg are strongly determined by CEC in these soils (Gilliam and Turrill, 1993; Gilliam et al., 1994). By contrast, significant correlations for herbaceous layer H' were positive and associated with other soil variables (i.e. clay content and organic matter) (Table 4).

These results are consistent with conclusions of Pausas (1994) working in Pyrenean pine forests, who found that stand structural variables such as those studied here exert less influence on herb species diversity than do site quality variables. In their comparison of 40-year-old mixed conifer plantations to old-growth stands of similar species on Vancouver Island, Qian et al. (1997) found that canopy characteristics had minimal influences on herbaceous layer species richness, diversity (H'), and evenness (J').

5. Conclusion

Clearcutting had no significant effects on species richness and diversity of the herbaceous layer following 20 years of post-harvest recovery at FEF and there were no significant changes in site quality measured as organic matter, cation exchange capacity, and extractable nutrients. This has important implications for forest management in the context of the National Forest Management Act of 1976, which mandates that management prescriptions should preserve diversity of plant and animal communities (Roberts and Gilliam, 1995a). Data presented here suggest that clearcutting in central Appalachian hardwood forests, if carried out properly, is consistent with the language of this mandate.

The herbaceous layer appeared to respond to stand structural and site quality variables in ways that varied between clearcut and mature stands. Herbaceous layer richness was sensitive to stand structure in clearcut stands, but much less so in mature stands. Plots with higher cover in clearcut areas had more species present, rather than more cover of a few species. In contrast, richness was not related to cover in mature stand plots.

Finally, species richness of the herbaceous layer on both clearcut and mature stands exhibited relationships with stand structure and site factors that were different from those between species diversity and structure/site factors. Thus, the terms ‘richness’ and ‘diversity’ often used interchangeably in the literature clearly are not synonymous for the herbaceous layer of these central Appalachian hardwood forests.

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