Herbaceous-Layer and Overstory Species in Clear-cut and Mature Central Appalachian Hardwood Forests

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HERBACEOUS-LAYER AND OVERSTORY SPECIES IN CLEAR-CUT AND MATURE CENTRAL APPALACHIAN HARDWOOD FORESTS[1,2]

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Abstract. The current interest among resource managers in ecosystem management necessitates a better understanding of the response of plant species diversity to forest management practices. This study attempted to assess the effects of one forest management practice—clear-cutting—on plant biodiversity in a mid-Appalachian hardwood forest by comparing species composition and diversity between two young ($\approx$20 yr following clear-cutting) and two "mature" (>70 yr following selective cutting) watersheds. Sampling was confined to the herbaceous layer (vascular plants $\leq$1-m in height) and woody overstory (stems $\geq$2.5 cm diameter at 1.5-m height). The important tree species occurred on all watersheds, but the relative importance of these species varied greatly with stand age. Less shade-tolerant species, such as black cherry (*Prunus serotina*) and tulip poplar (*Liriodendron tulipifera*), are replaced by more-tolerant species, such as northern red oak (*Quercus rubra*) and sugar maple (*Acer saccharum*), as the stand matures. Analysis of tree species richness per plot suggests that the competitive thinning process decreases species evenness as the stand develops. Important herb-layer species included stinging nettle (*Laportea canadensis*), violets (*Viola* spp.), seedlings of striped maple (*A. pensylvanicum*), and several fern species. In sharp contrast with the trees, these species appeared to vary little with stand age. Species diversity (H') did not vary with stand age for either the overstory or the herbaceous layer. Detrended correspondence analysis showed a significant correlation between species composition of the two strata for the mature watersheds, but not the young, clear-cut watersheds. Thus, we suggest a temporal shift in processes influencing species composition following disturbance from allogenic factors (e.g., soil characteristics) to autogenic factors (e.g., stand characteristics), which lead to a linkage between forest strata later in succession. The degree to which forest management alters species composition in these central Appalachian forest ecosystems may be tied to the degree of alteration of the link between strata.

Key words: clear-cutting; Eastern deciduous forest; Fernow Experimental Forest, West Virginia; forest management effects; herbaceous layer; relationships between forest strata; shade tolerance; species diversity; succession.

Introduction

In 1992 the USDA Forest Service initiated a policy of "ecosystem management," mandating that the agency take "an ecological approach to multiple-use management . . . that blends the needs of the people and the environment" (Bartuska 1993). Among the many departures from past practices that this new policy establishes is a focus away from "important" species as determined solely by the commercial value of trees and towards an ecosystem perspective that places an "ecological" value on all forest species, whether woody or herbaceous, plant or animal. Thus, the response of species composition and diversity of the forest as a whole (not just the woody overstory) to forest management practices has become increasingly relevant. Indeed, Franklin (1993) argued that an ecosystem approach to addressing diversity questions is necessary to fully understand impacts of human activity in the context of global sustainability. Recent studies have considered trade-offs between economic returns of a variety of forest management activities and diversity in eastern forests (Smith and Miller 1987, Niese and Strong 1992, Lu and Buongiorno 1993).

Past land-use practices throughout the eastern United States have resulted in secondary forests in most of the region. However, despite the heavy cutting and fires

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[1] Manuscript received 2 March 1994; revised 25 August 1994; accepted 9 October 1994; final version received 28 November 1994.

[2] For reprints of this 67-page group of papers on plant diversity in managed forests, see footnote 1, page 911.

TABLE 1. Physical characteristics of four watersheds (WS) of the Fernow Experimental Forest, West Virginia, USA.

Variable	WS7	WS3	WS13	WS4
Stand age (yr)	≈20; even-aged	≈20; even-aged	>70; mixed-age	>80; mixed-age
Stand history	Clear-cut; herbicide	Clear-cut; acidification	Select cut	Select cut
Area (ha)	24.2	34.3	14.2	38.7
Aspect	E-NE	S	E-NE	S-SE
Elevation (m)	725–850	735–860	735–805	750–870

that characterized the period of railroad logging from ≈1880 to 1930 (Marquis and Johnson 1989), many eastern hardwood forests are still typically species-rich, a characteristic that can be attributed to many factors, such as relatively high availability of essential resources. Another factor would be the vertical heterogeneity of the physical structure of forests (i.e., the formation of the several forest strata), which results from an interaction of plant species' life histories and competition. In addition to the obvious significance of the woody overstory in forests, the herbaceous layer plays an important role in initiating competition among seedling and sprouting individuals of potential overstory dominants. Also, due to its sensitivity to soil fertility and site conditions (Siccama et al. 1970, Peterson and Rolfe 1982, Gilliam 1988), the herb layer has been used as an indicator of general edaphic factors and forest site quality (Pregitzer and Barnes 1982, Cserep et al. 1991, Strong et al. 1991). The herb layer also exhibits sensitivity to a variety of forest disturbances (Moore and Vankat 1986), including forest management practices (Duffy and Meier 1992).

Gilliam et al. (1994) viewed the herb layer as a dynamic assemblage of resident and transient species, with resident species being those plants, such as annuals, herbaceous perennials, and low-growing shrubs, whose life history characteristics confine them to this stratum. In contrast, the transient species are plants, such as larger shrubs and trees, which have the potential to eventually emerge into higher strata. Many authors have reported significant relationships between overstory and herbaceous strata, citing several factors to explain this linkage (Gagnon and Bradfield 1987, Roberts and Christensen 1988, Host and Pregitzer 1992), whereas other authors have emphasized the possibility that apparent linkages between strata can result from an artifact of β-diversity across large sample areas (Bratton 1975, McCune and Antos 1981). Mechanisms behind such linkages may be related to the response of strata to disturbances, including forest management practices.

Forest management systems commonly used throughout the eastern deciduous forest represent a gradient of disturbance intensity, from the least intense with single tree selection (harvesting of individual selected trees from most or all size classes) to the most intense with clear-cutting (complete removal of the stand in a single harvest) (Marquis and Johnson 1989). The relationship between harvest (disturbance) intensity and woody species response is reasonably well established, with regeneration of tolerant species being favored by low-intensity methods and less shade-tolerant species favored by high-intensity methods (Marquis and Johnson 1989). The response of the herbaceous layer to various forest management practices, however, is less well known (Gilliam and Turrill 1993).

This paper focuses on the effects of one of these forest management systems—clear-cutting—on forest species composition and diversity in central Appalachian hardwood forest ecosystems. The following questions are addressed: (1) What is the effect of clear-cutting on plant species composition and diversity? (2) How do patterns of overstory species composition and diversity vary among experimental watersheds? (3) How do patterns of herbaceous-layer species composition and diversity vary among experimental watersheds? and (4) Is species composition related between these forest strata, and, if so, how is this relationship influenced by treatment?

MATERIALS AND METHODS

Study site

This study was carried out at the Fernow Experimental Forest (FEF), a ≈1900-ha area of largely montane hardwood forests in the Allegheny Mountain section of the unglaciated Allegheny Plateau, located in Tucker County, north-central West Virginia (Forest Service 1987). Mean annual precipitation is ≈1430 mm/yr, with most precipitation occurring during the growing season (Gilliam et al. 1994). Four contiguous watersheds (WS) were selected for this study (Table 1): WS7 and WS3 are ≈20-yr-old, even-aged stands following clear-cutting; WS13 and WS4 are uneven-aged stands (>70 yr old—hereafter "mature" watersheds). WS7 and WS3 further differ in stand history, with WS7 being cut between 1963 and 1967 and maintained barren with herbicide until late 1969; WS3 was clear-cut to a diameter at breast height (dbh) limit of 2.5 cm in 1970 (Table 1). WS3 has also received acidification applications of $(NH_4)_2SO_4$ since 1989 (Gilliam et al. 1994).

Study watersheds support primarily mixed-hardwood stands. The herbaceous layer is quite heterogeneous along elevation gradients in all stands (Gilliam and Turrill 1993). Watersheds are similar in most other respects, with the exception of aspect: WS7 and WS13 are north-facing, whereas WS3 and WS4 are south-

TABLE 2. Stand characteristics of four watersheds (WS) of Fernow Experimental Forest, West Virginia, USA. Means followed by the same lower-case superscript letter are not significantly different between watersheds at $P < 0.05$.

Variable	WS7	WS3	WS13	WS4
Density (stems/ha)	1788^b	2410^a	760^c	948^c
Basal area (m²/ha)	20.0^b	25.0^b	45.5^a	40.0^a
Richness (sp./plot)	7.5^a	7.4^a	5.4^b	6.7^{ab}
Total richness, S*	19	15	18	22
Diversity, H'†	0.89	0.74	0.75	0.88
Equitability, J‡	0.30	0.27	0.26	0.28

* Total number of species encountered in sample plots for each watershed.

† Shannon-Wiener Index, using ln-transformations of whole-watershed data.

‡ $J = H'/\ln S$ (Begon et al. 1990).

facing (Table 1). Soils are similar among all four watersheds. These are relatively thin (<1 m in depth), acidic, sandy-loam Inceptisols of two series: Berks (loamy-skeletal, mixed, mesic Typic Dystrochrept) and Calvin (loamy-skeletal, mixed, mesic Typic Dystrochrept) (Forest Service 1987). Previous studies have found no significant differences among these watersheds, regardless of stand age, in soil texture (67% sand, 11% clay, and 22% silt for all watersheds combined), organic matter (13.8%), and cation exchange capacity (44 mmol_c/kg) (Turrill 1993, Gilliam et al. 1994). These studies have also shown surprisingly few differences in extractable nutrients among our study watersheds.

It should be noted that, while WS3 and WS7 each received a commercial clearcut, they also have received additional treatment since clear-cutting as part of different Forest Service projects being carried out at FEF (Table 1). However, although these treatments might conceivably have altered species composition on their respective watersheds, we are assuming for our comparisons that subsequent treatments have had minimal effects on species. We feel justified in this assumption for the following reasons: (1) It is highly unlikely that the 2–3 yr of acidification on WS3 would change the composition of the overstory in this short time period. Indeed, herbaceous-layer species composition should be much more sensitive to this treatment, but it has been established that acidification has had no significant effect on the herb-layer composition of WS3 (Gilliam et al. 1994). (2) There were few differences between WS3 and WS7 that were attributable to the herbicide treatment on WS7, the cessation of which initiated stand development (Table 2). Plant growth immediately following release from herbicide was substantial on WS7 in 1970 (Kochenderfer and Wendel 1983).

Field sampling

Fifteen circular sample plots (0.04 ha in area per plot) were established in each of the study watersheds; all stems ≥2.5 cm in diameter at breast height (dbh, ≈1.5 m) in each plot were tallied, identified, and measured for dbh to the nearest 0.1 cm. In all, ≈3500 stems were measured. The herbaceous layer was sampled by estimating cover of all vascular plants ≤1 m in height within 10 1-m² circular sub-plots in each sample plot. The 10 sub-plots were located within each sample plot using a stratified-random polar coordinates method (Gaiser 1951) to avoid over-sampling the inner one-half of the plot area. All vascular plants ≤1 m in height within the sub-plots were identified and measured for cover using a visual estimation method as described in Gilliam and Turrill (1993).

Data analysis

Watershed means were compared using analysis of variance and Duncan's multiple-range testing (Ray 1982, Zar 1984). Importance values (IVs) of overstory species in each watershed were calculated as the sum of relative basal area and relative density. Importance values of herbaceous-layer species in each watershed were calculated as the sum of relative cover and relative frequency. Species diversity was calculated as the Shannon-Weiner Index (H') using ln-transformed IV data for each stratum. Due to differences in spatial variability between strata, watershed H' was calculated as a mean of the 15 individual-plot H' values for the herbaceous layer, whereas H' for the overstory was calculated from whole-watershed IV data.

Species data for overstory and herbaceous strata were analyzed with two multivariate techniques. Input data for each method were ln-transformed IVs from each sample plot. Canonical discriminant analysis (CDA; Ray 1982: procedure CANDISC) was used to focus on species' differences between watersheds and to determine successional sequences for each strata. CDA combines canonical correlation with principal components analysis to ordinate and compare more than a single data matrix (Gilliam et al. 1993). For our analyses, each watershed represented a single matrix, for a total of four data matrices.

Detrended correspondence analysis (DCA) was used to examine species' turnover with respect to stand age for both the overstory and herbaceous layer (ter Braak 1987, 1990). Species composition was compared between strata by correlating scores of DCA axes of each strata that best represented an age gradient.

RESULTS AND DISCUSSION

In comparing the two clear-cut to the two mature watersheds, we are following the conceptual model of Bormann and Likens (1979), which divides forest development into four phases: (1) reorganization, a 10–20 yr period in which total ecosystem biomass declines despite increases in living biomass; (2) aggradation, a >100-yr period in which total ecosystem biomass increases to a maximum toward the end of the period; (3) transition, a variable period of time when total bio-

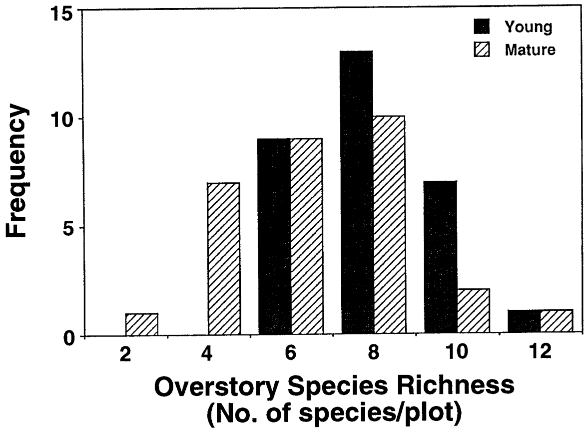

FIG. 1. Frequency distribution of overstory species richness in young (20 yr old) vs. mature (>70 yr old) hardwood stands of Fernow Experimental Forest, West Virginia, USA. Bars represent number of sample plots in each richness class, defined as the total number of species per 0.04-ha plot.

mass declines; and (4) steady state, an equilibrium period when biomass fluctuates around a mean level.

Although Bormann and Likens (1979) were clear in their discussion of steady-state forest maturity, they provided no real examples for a point of comparison (Reiners 1992). In his study at Hubbard Brook Experimental Forest, Reiners (1992) compared a 20-yr-old watershed (W2) to a "mature" 55-yr-old watershed (W6). In our study WS13 and WS4 are each at least 70 yr old and have attained a mixed-age status. Thus, we refer to them as "mature" (sensu Reiners 1992) and estimate that they are toward the end of the aggradation phase. Our 20-yr-old clear-cut watersheds may be either at the end of the reorganization phase or at the beginning of the aggradation phase.

Woody overstory

Stem density was much higher in the young, clear-cut stands (≈2000 stems/ha) compared to the mature stands (≈800 stems/ha) (Table 2). Basal area in the young stands, on the other hand, was only about one half that of the mature stands (Table 2), consistent with what we would expect of 20-yr-old stands during the competitive thinning process; that is, high densities of small stems giving way to lower densities of much larger stems. Our 20-yr-old stands had a lower tree density and higher tree basal area than a 20-yr-old stand at Hubbard Brook, which had 2730 stems/ha and 14.3 m^2/ha, respectively (Reiners 1992).

There are several ways in which to describe the species structure of the experimental watersheds. Total species richness for watersheds as a whole (*S*, all species found in the 15 sample plots in each watershed) showed little variation with stand age, with perhaps a slight tendency toward more species in mature stands (Table 2). The young stands, however, had a significantly higher species richness on a per-plot basis. This suggests that the fewer species that may be encountered in the young stands are more evenly distributed throughout the watershed and that competitive thinning results in a more patchy distribution (lower equitability) of species in mature watersheds. Shannon-Weiner indices (using ln-transformations of whole-watershed data) showed no consistent difference associated with stand age (Table 2).

TABLE 3. Important overstory species of four watersheds (WS) of Fernow Experimental Forest, West Virginia, USA. Data are importance values based on sum of relative basal area and relative density. Nomenclature follows Gleason and Cronquist (1991).

Species	WS7	WS3	WS13	WS4
Acer pensylvanicum	4.4	4.5	···	9.7
A. saccharum	44.3	33.7	104.7	74.7
Betula lenta	37.4	···	···	···
Fagus grandifolia	···	9.6	8.5	18.7
Fraxinus americana	12.3	7.9	3.8	···
Liriodendron tulipifera	20.7	10.4	8.2	2.2
Prunus serotina	51.0	100.9	26.2	13.1
Quercus prinus	···	···	14.5	8.9
Q. rubra	2.7	11.4	17.2	43.6
Robinia pseudoacacia	11.5	···	···	···
Sassafras albidum	5.3	6.8	···	···

Both stand types showed a central tendency for species richness per plot, with the mean for clear-cut stands >7 species/plot and the mean for mature stands around 6 species/plot (Fig. 1). A high proportion (60%) of mature stand plots had ≤6 species/plot, and a high proportion (70%) of clear-cut stand plots contained ≥8 species/plot. Thus, considering the total richness values of clear-cut stands in Table 2, many plots in these stands have more than two thirds of the species of the entire ≈30-ha watershed in a 0.04-ha sample plot area.

Overstory species composition was similar among the watersheds, regardless of stand age, with the four most important species being found in all watersheds (Table 3); these were sugar maple (*Acer saccharum* Marsh.), yellow poplar (*Liriodendron tulipifera* L.), black cherry (*Prunus serotina* Ehrh.), and northern red oak (*Quercus rubra* L.). Importance was based on importance values, IVs, the sum of relative basal area and relative density. The relative importance of these species, however, appeared to vary substantially with stand age.

To determine a successional sequence for these watersheds, we used canonical discriminant analysis (CDA) on per-plot IVs (following ln-transformation) of all overstory species (Fig. 2). Axis 1 appeared to correspond well with stand age, with clusters of plots from WS7 and WS3 found at the positive end of the axis, and those from WS13 and WS4 toward the negative end (Fig. 2).

Based on canonical correlations with Axis 1, black cherry, yellow poplar, and black locust loaded highly on the positive end of the axis, whereas sugar maple, northern red oak, and beech loaded highly on the neg-

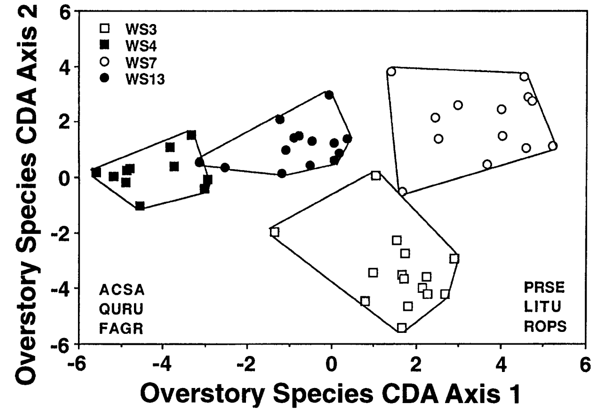

FIG. 2. Ordination of overstory species data from four watersheds (WS) in Fernow Experimental Forest (West Virginia, USA) using canonical discriminant analysis (CDA). Each point on the figure represents a single sample plot. Species with high positive loadings on Axis 1 were *Prunus serotina* (PRSE), *Liriodendron tulipifera* (LITU), and *Robinia pseudoacacia* (ROPS). Species with high negative loadings on Axis 1 were *Acer saccharum* (ACSA), *Quercus rubra* (QURU), and *Fagus grandifolia* (FAGR).

TABLE 4. Herbaceous-layer characteristics of four watersheds of Fernow Experimental Forest, West Virginia, USA. Means followed by the same lower-case superscript letter are not significantly different between watersheds at $P < 0.05$.

Variable	WS7	WS3	WS13	WS4
Cover (%)	37.5^{a}	19.3^{b}	17.9^{b}	26.4^{b}
Biomass (g/m^{2})*	18.5^{a}	9.7^{b}	9.1^{b}	13.3^{b}
Richness (sp./plot)†	15.3^{a}	11.5^{b}	13.5^{ab}	12.1^{b}
Total richness, *S* (sp./watershed)	64	40	62	45
Diversity, *H′*	1.6^{a}	1.9^{a}	1.2^{b}	1.9^{a}

* Values based on regression equations from Gilliam and Turrill (1993).

† Total number of species encountered in sample plots for each watershed.

ative end of the axis, suggesting a successional sequence with less shade-tolerant species (e.g., black cherry and yellow poplar) being replaced by the tolerant species, such as sugar maple and northern red oak. This is consistent with hypothetical trends among shade-tolerance classes proposed by Bormann and Likens (1979), who focused on "exploitive" vs. "conservative" strategies among tree species' responses following clear-cutting. Their sequence predicted rapidly increasing dominance of intolerant species (exploitive strategy), followed by sharp declines <20 yr after clear-cutting. Tolerant species (conservative strategy) increase in dominance slowly after ≈20 yr (Bormann and Likens 1979).

Herbaceous layer

With the exception of a few characteristic species of WS7, the herbaceous layer was surprisingly similar among the study watersheds. There were no significant differences ($P < 0.05$) among WS3, WS13, and WS4 for cover, biomass (calculated from cover, see Gilliam and Turrill 1993), or species richness (Table 4). Significant differences between WS7 and the other watersheds for cover and biomass were due to the high cover of two fern species and are likely the result of slope aspect (north-facing), which favors these fern species (Phillippi and Boebinger 1986, Aulick 1993, Gilliam et al. 1994). The generally higher species richness values per plot for WS7 and WS13 (Table 4) may have been related to the higher total richness for these watersheds, compared to WS3 and WS4. Total watershed richness differences, in turn, may have been the result of aspect differences among the watersheds, with WS7 and WS13 having a more north-facing aspect and WS3 and WS4 having a more south-facing aspect (Table 1). In contrast to patterns of overstory species richness (Fig. 1), frequency distributions for numbers of herb-layer species per plot showed neither a central tendency, nor a difference with stand age (Fig. 3).

With the exception of dominance by ferns such as shield fern (*Dryopteris marginalis* (L.) Gray) and Christmas fern (*Polystichum acrostichoides* (Michx.) Schott) on WS7, species composition was quite similar among watersheds, regardless of stand age (Table 5). The more important species were stinging nettle (*Laportea canadensis* (L.) Wedd.), species of violet (*Viola* L. spp.), greenbrier (*Smilax rotundifolia* L.), species of blackberry (*Rubus* L. spp.), and seedlings of striped maple (*A. pensylvanicum* L.) and black cherry (Table 5).

The high degree of similarity among watersheds with respect to herbaceous-layer species composition is also supported by the results of CDA (Fig. 4). Again, the predominance of the ferns became apparent, distinguishing WS7 from the other watersheds, which were closely clustered toward the middle of Axis 1. Indeed, in contrast to the results of CDA for overstory data

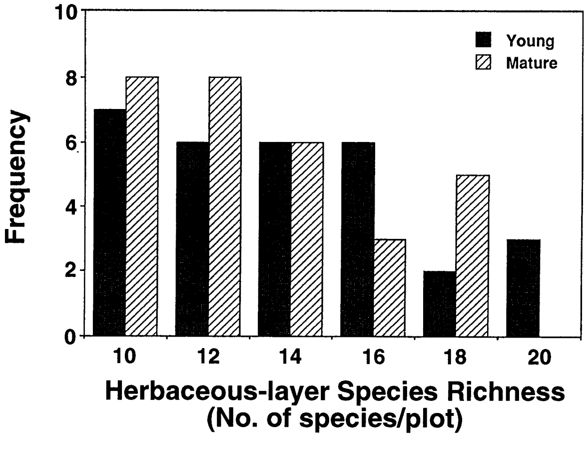

FIG. 3. Frequency distribution of herbaceous-layer species richness in young (20 yr old) vs. mature (>70 yr old) stands of Fernow Experimental Forest, West Virginia, USA. Bars represent number of sample plots in each richness class, defined as the total number of species per 0.04-ha plot.

TABLE 5. Important herbaceous-layer species of four watersheds (WS) of Fernow Experimental Forest, West Virginia, USA. Data are importance values based on sum of relative cover and relative frequency. Nomenclature follows Gleason and Cronquist (1991).

Species	WS7	WS3	WS13	WS4
Acer pensylvanicum	···	14.7	19.0	15.5
Dryopteris marginalis	52.8	6.2	3.7	7.9
Laportea canadensis	7.2	26.8	20.9	33.9
Polygonatum biflorum	···	···	11.0	9.4
Polystichum acrostichoides	17.2	···	18.5	11.0
Prunus serotina	4.9	13.2	···	9.3
Rubus spp.	10.2	13.2	···	7.8
Sassafras albidum	5.7	10.0	···	···
Smilax rotundifolia	7.5	21.3	8.5	9.3
Viola spp.	14.8	24.4	25.6	14.5

(Fig. 2), Axis 1 for the herb layer appeared unrelated to stand age (Fig. 4).

Interactions between overstory and herbaceous strata

Consistent with the ecosystem perspective related to "ecosystem management," this study focused not only on the response of the overstory and herbaceous layers to disturbance separately, but also on the interaction of these strata and how the interaction itself might respond to clear-cutting. Strata interactions may be assessed in several ways, but a common method is to compare (correlate) axis scores from ordinations of species data from each stratum (Roberts and Christensen 1988, Host and Pregitzer 1992). This is essentially testing to see if variation in species composition in each stratum is responding to the same gradient. Examination of strata interactions is quite important in the context of ecosystem management because it focuses more on how the forest system as a whole might respond to management treatments, rather than on just the dominant overstory species. Although it is not within the scope of this study to do so, such a focus on interactions might be applied also to other components of the forest ecosystem, e.g., plant–herbivore (including invertebrates) and other trophic interactions (Franklin 1993).

Although CDA was useful in comparing species similarities/differences among watersheds (Figs. 2 and 4), a more appropriate way to look at overall species composition of each forest stratum and actual species compositional changes with respect to environmental gradients (e.g., stand age) is through the use of detrended correspondence analysis (DCA) (Gauch 1982). Because of the "units" of the DCA axes (SD—average standard deviation of species turnover; Gauch 1982), DCA ordinations allow for a direct assessment of β-diversity and gradient lengths among the watersheds. We performed DCA on each stratum separately and then correlated axis scores to assess relationships between strata.

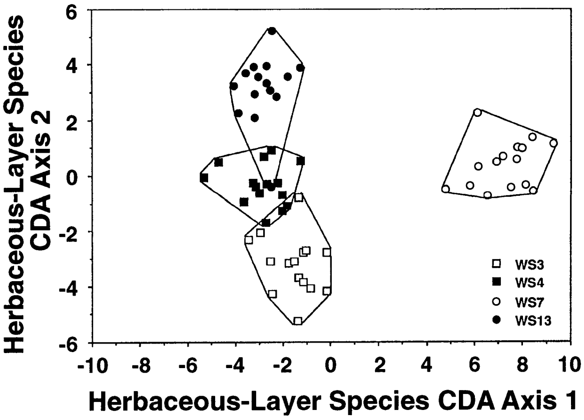

FIG. 4. Ordination of herbaceous-layer species data from four watersheds (WS) in Fernow Experimental Forest (West Virginia, USA) using canonical discriminant analysis (CDA). Each point on the figure represents a single sample plot.

For the overstory, DCA Axis 1 appeared to be well correlated with stand age, with plots of the young, clear-cut stands located generally toward the low end and plots of mature stands toward the high end (Fig. 5). Notably, there was an appreciable degree of overlap involving approximately one third of the plots from each stand type (clear-cut vs. mature). β-diversity (indicated by axis length) was somewhat lower than might have been expected of plots from stands differing so greatly in age. This supports conclusions based on important species (Table 3) that overstory species composition is quite similar among watersheds.

The initial ordination of the herbaceous-layer species data produced an outlier from WS3 which was >1 half-change from the rest of the data along DCA Axis 2 and caused these points from WS3 to be greatly compressed. The outlier was a plot that had a disproportionately high cover (nearly 100%) of a single species, ground cedar (*Lycopodium flabelliformes* Fern.). Such an outlier warranted a second ordination with the outlier removed (Gauch 1982, Kent and Coker 1992). DCA Axis 1 length for the herbaceous layer was much great-

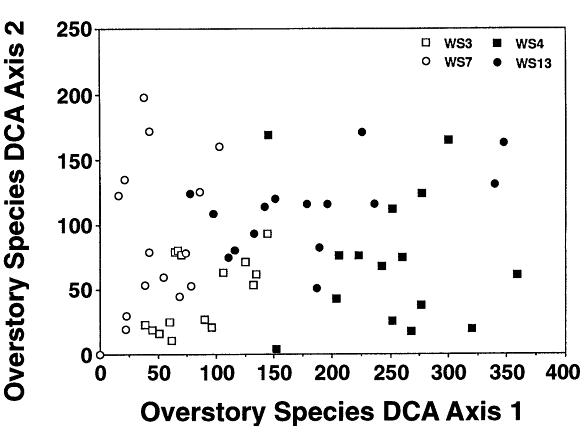

FIG. 5. Ordination of overstory species from four watersheds (WS) using detrended correspondence analysis (DCA). Each point on the figure represents a single sample plot.

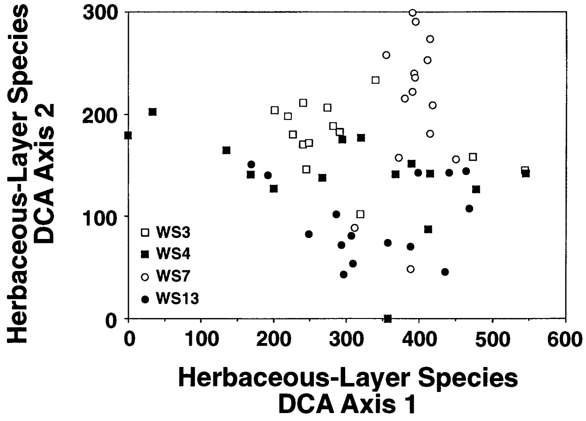

FIG. 6. Ordination of herbaceous-layer species from four watersheds (WS) using detrended correspondence analysis (DCA). Each point on the figure represents a single sample plot.

er than that for the overstory; however, it did not correlate well with stand age (Fig. 6). This suggests that variation in species composition of the herbaceous layer was greater within watersheds than among watersheds, confirming conclusions of Gilliam and Turrill (1993) who compared the herb layer on WS3 and WS4. DCA Axis 2 appeared better correlated with stand age than did Axis 1, with plots from the young, clear-cut stands (WS7 and WS3) occurring toward the high end and mature stands toward the low end of the axis (Fig. 6).

Axis scores of these DCA ordinations were compared (Pearson product-moment correlation) to examine species compositional relationships between the two forest strata. The main criterion for selection of axes for the comparison was how well the axes appeared to correlate with stand age. Therefore, we used DCA Axis 1 from the overstory ordination (Fig. 5) and, because it was better-correlated with stand age, DCA Axis 2 from the herbaceous-layer ordination (Fig. 6).

Correlations between overstory and herbaceous strata varied among watersheds, when the correlations were run for individual watersheds and stand types, and these variations were related to stand age (Fig. 7). Whereas overstory–herb-layer correlations were significant ($P < 0.05$) for each of the mature watersheds (WS13 and WS4), such correlations were not significant for either of the clear-cut watersheds.

Two additional questions that merit attention here are (1) What are possible mechanisms to explain these patterns of linkage of species composition between forest strata? and (2) How does linkage relate to the effects of management practices on species diversity of forest ecosystems? We hypothesize that this link is sensitive to the degree of initial disturbance and that the degree (intensity, as measured by significance of correlations) of linkage increases as the stand develops, at least in eastern hardwood forests.

Mechanisms of linkage between strata

Following clear-cutting in these forests, a single undifferentiated stratum (comprised of sprouts of woody and herbaceous perennials and seedlings from buried seeds) develops rapidly in response to sharp increases in essential resources (Bormann and Likens 1979, Gilliam and Turrill 1993). Using cut sections of forest floor grown under greenhouse conditions (which somewhat resemble post-harvest clearcut conditions) at Fernow Experimental Forest (FEF), Wendel (1987) found 44 species to develop from buried seed, rootstocks, and rhizomes. Among these were the dominant species for both the overstory and herbaceous strata found in this study (Tables 3 and 5). Competition between woody and herbaceous species for water and nutrients at this stage can be particularly intense (Morris et al. 1993, Wilson and Shure 1993). Intolerant woody species that survive competition then exhibit rapid height growth and increased foliar cover (Bormann and Likens 1979). Indeed, during the first 10 yr following clear-cutting and herbiciding on WS7 at FEF, Kochenderfer and Wendel (1983) found that, while herbaceous species cover decreased from ≈60% to <5%, woody species cover increased from <5% to >80%.

From clear-cutting to ≈20 yr later the two strata are responding to different sets of environmental gradients; thus, one would not expect to find a significant linkage between the two. Species composition of the overstory at this 20-yr point in post-harvest response is determined largely by competitive ability to exploit light availability (exploitive strategy, sensu Bormann and Likens 1979). At this same time, herbaceous-layer development is being controlled largely by availability of water and nutrients (Morris et al. 1993, Wilson and Shure 1993). Working with WS3 and WS4 at FEF, Gilliam and Turrill (1993) found that the herb layer cor-

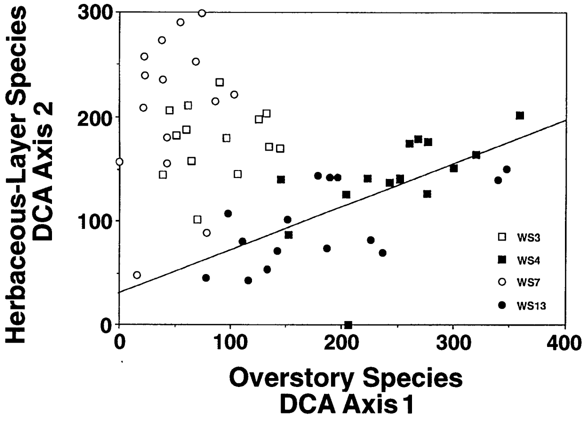

FIG. 7. Correlation between overstory and herbaceous-layer species composition. Overstory is represented on the x axis as DCA Axis 1 from Fig. 5; herbaceous layer is represented on the y axis as DCA Axis 2 from Fig. 6. Each point on the figure represents a single sample plot. The line shown is for mature stand plots (closed symbols) only. Equation is: $y = 28.86 + 0.41x$; $r^2 = 0.44$, $P < 0.001$.

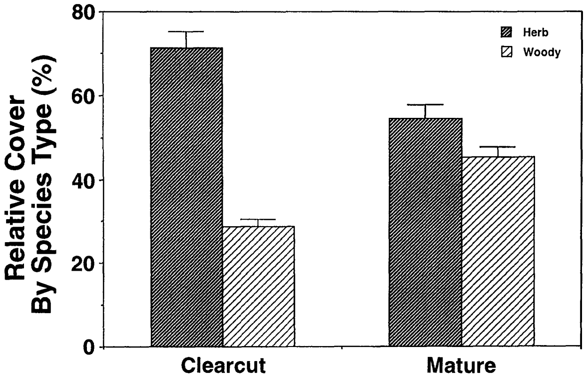

FIG. 8. Comparisons of relative cover of herbaceous vs. woody species of the herbaceous layer in stands 20 yr after clear-cutting and in mature (>70 yr old) stands. Means + 1 SE for clear-cut stands include all plots of WS3 and WS7; means + 1 SE for mature stands include all plots of WS4 and WS13. Means for both herb and woody species data are different between stand types at $P < 0.01$. Differences between herb vs. woody plants were significant ($P < 0.05$) for both clear-cut and mature stands.

related with virtually all measured soil variables (e.g., pH, texture, organic matter, cation exchange capacity, extractable cations, and NO_3^-) on the young, clear-cut watershed (WS3), whereas the herb layer correlated with virtually no soil variables on WS4.

Later in post-harvest recovery, overstory dominance changes toward more shade-tolerant species that can maintain slow growth beneath the initial woody canopy (conservative strategy, sensu Bormann and Likens 1979). These species create quite different canopy conditions (closed and stratified), greatly altering the light regime for the herb layer. As light becomes more limiting, these conditions favor the success of seedlings and sprouts of woody species (Wilson and Shure 1993), which increase in importance within the herbaceous layer. At FEF we found that, whereas the herbaceous component of the herb layer was significantly ($P < 0.001$) higher in young, clear-cut stands than in mature stands, the woody component of the herb layer was significantly higher in the mature stands (Fig. 8). In fact, although herbaceous species represented ≈70% of the herb layer in clear-cut stands, the herb layer of mature stands was approximately equally balanced between herbaceous and woody species cover (Fig. 8).

In addition to canopy-mediated changes in light availability to the forest floor, the temporal shift in herbaceous–woody species cover (e.g., Fig. 8) likely arises from increases in numbers of juveniles developing from seeds produced by the overstory species. Late-successional species in these forests are prolific seed-producers, explaining the high densities of large numbers of tree species that Wendel (1987) found germinating from cut sections of forest floor at FEF. Therefore, the herb layer and overstory begin to respond more to similar environmental gradients and the linkage between the two strata, as illustrated in Fig. 7, intensifies.

Implications for forest management effects

The degree to which forest management alters species diversity in these central Appalachian forest ecosystems may be tied to the degree of alteration of this link between forest strata. Therefore, we would expect that the disturbance intensity gradient represented by the management practices used in this region (Marquis and Johnson 1989) may result in a gradient of effects on this linkage, with single-tree selection having the least effect. Effects of clear-cutting on species composition and diversity at FEF were largely related to successional change initiated by the disturbance and a complete "decoupling" of the relationship between overstory and herbaceous layer.

Using some of the indices of measuring richness and diversity, it might be concluded that there were minimal effects associated with clear-cutting, at least for the time interval of ≈60 yr examined in this study. However, there appeared to be a shift during this time period in processes that control species composition and diversity following forest disturbance. This represents a shift from those that might be considered allogenic toward those that are more autogenic, ultimately leading to a linkage between forest strata later in succession. Although the mature stands used in this study are likely representative of most of the older stand ages of secondary forests of the central Appalachian region, it would be possible to test this hypothesis further if older stands could be found.

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