

Effects of atmospheric nitrogen deposition on the herbaceous layer of a central Appalachian hardwood forest

Frank S. Gilliam¹ and Anne W. Hockenberry

Department of Biological Sciences, Marshall University, Huntington, WV 25755-2510

Mary Beth Adams

U.S.D.A. Forest Service, Timber and Watershed Laboratory, Parsons, WV 26287-0404

GILLIAM, F. S., A. W. HOCKENBERRY (Department of Biological Sciences, Marshall University, Huntington, WV, 25755-2510), AND M. B. ADAMS (U.S.D.A. Forest Service, Timber and Watershed Laboratory, Parsons, WV, 26287-0404). Effects of atmospheric nitrogen deposition on the herbaceous layer of a central Appalachian hardwood forest. *J. Torrey Bot. Soc.* 133(2): 240–254. 2006.—Additions of nitrogen (N) have been shown to alter species diversity of plant communities, with most experimental studies having been carried out in communities dominated by herbaceous species. We examined seasonal and inter-annual patterns of change in the herbaceous layer of two watersheds of a central Appalachian hardwood forest that differed in experimental N treatment. This study was carried out at the Fernow Experimental Forest, West Virginia, using two adjacent watersheds: WS4 (mature, second-growth hardwood stand, untreated reference), and WS3 (~25-yr old, treated with 35 kg N ha⁻¹ yr⁻¹ as (NH₄)₂SO₄ yr⁻¹). Seven circular 0.04-ha sample plots were established in each watershed to represent its full range of elevation and slope aspect. The herbaceous layer was sampled by identifying and visually estimating cover (%) of all vascular plants ≤ 1 m in height within 10 1-m² circular sub-plots in each sample plot, for a total of 140 1-m² sub-plots. Sampling was carried out in mid-July of 1991 and repeated at approximately the same time in 1992. In 1994, these same plots were sampled each month from May to October. Seasonal patterns of herb layer dynamics were assessed for the complete 1994 data set, whereas inter-annual variability was based on plot data from 1991, 1992, and the July sample of 1994. There were no significant differences between watersheds for any sample year for any of the other herb layer characteristics measured, including herb layer cover, species richness, evenness, and diversity. Cover on WS4 decreased significantly from 1991 to 1992, followed by no change to 1994. By contrast, herb layer cover did not vary significantly across years on WS3. Cover of the herbaceous layer of both watersheds increased from early in the growing season to the middle of the growing season, decreasing thereafter, with no significant differences between WS3 and WS4 for any of the monthly cover means in 1994. Similar seasonal patterns found for herb layer cover—and lack of significant differences between watersheds—were also evident for species diversity and richness. By contrast, there was little seasonal change in herb layer species evenness, which was nearly identical between watersheds for all months except October. Seasonal patterns for individual species/species groups were closely similar between watersheds, especially for *Viola rotundifolia* and *Viola* spp. Species richness and species diversity were linearly related to herb layer cover for both WS3 and WS4, suggesting that spatial and temporal increases in cover were more related to recruitment of herb layer species than to growth of existing species. Results of this study indicate that there have been negligible responses of the herb layer to 6 yr of N additions to WS3.

Key words: eastern deciduous forest, forest ecosystems, forest strata, herbaceous layer, nitrogen deposition, seasonal patterns.

Experimental studies examining the effects of nitrogen (N) on species diversity of plant communities have a long history, with the first and possibly best known study being the Park Grass Experiment in Rothamsted, England (see Richardson 1938 for an early reference). More recent studies at the Cedar Creek Natural Area in Minnesota (e.g., Tilman 1987) confirm results of this earlier work—excess N can profoundly alter species composition and decrease species diversity of plant communities. Whereas most such studies have been carried out on herb-dominated

communities, far fewer have been done in forested ecosystems (Bobbink et al. 1998). This is a significant discrepancy, however, considering that forests (1) often occupy areas receiving high rates of atmospheric deposition of N (e.g., eastern U.S. and central Europe), and (2) generally display great structural complexity, with most of their species diversity occurring in the lowest stratum of vegetation—the herbaceous layer (see Gilliam and Roberts 2003a for commonly-used synonyms).

The time of response of plant communities to experimental additions of N can vary, with some plant communities exhibiting rapid responses. For example, Tilman (1987) reported significant changes in species composition of Minnesota

¹ E-mail: gilliam@marshall.edu

Received for publication March 7, 2005, and in revised form September 26, 2005.

Table 1. Characteristics of study watersheds of the Fernow Experimental Forest, WV.

Variable	WS3	WS4
Stand age (yr)	~25, even-aged	>90, mixed-age
Stand history	clearcut/N additions	select cut
Area (ha)	34.3	38.7
Aspect	S	S-SE
Elevation (m)	735-860	750-870
Cumulative N deposition, 1989-1994 (kg ha ⁻¹)		
Ambient	53	53
Added	210	0
Total	263	53
Tree density (stems/ha)	2410	948
Tree basal area (m ² ha ⁻¹)	25.0	40.0

old-fields to all levels of N additions within the first year following initiation of treatment. In fact, N treatments at this site have led to highly significant responses of species in every year of the study, although the specific pattern of response has varied inter-annually (Tilman 1989). Not all N-addition studies, however, have shown such an immediate response. Although Huberty et al. (1998) found that N additions increased plant biomass of Michigan old-fields, there were no significant changes in species composition or diversity over the seven-year period of the study.

Herb layer plants are generally sensitive to soil fertility, both in terms of growth and foliar nutrient content (Muller 2003), and some species have even been used as indicators of fertility (Pregitzer and Barnes 1982). Herb layer communities have been shown to change through successional time in response to changes in soil nutrients, including N and cations (Christensen and Gilliam 2003). It might be expected, however, that the herb layer of forests may display a lag-response to experimental additions of N, given the structural complexity of forest ecosystems, wherein resource availability can be greatly altered by other vegetation strata.

Indeed, Gilliam et al. (1994) concluded that experimental additions of N to a watershed at the Fernow Experimental Forest, West Virginia, had no significant effects on the herb layer composition, biomass, and foliar nutrients after 3 yr of treatment. Among the practical, interpretive limitations of that study, however, are that (1) although it was carried out at the height of the growing season, it based on a one-time sampling of the herb layer, precluding examination of seasonal patterns, and (2) it provided only a three-year assessment of N treatment effects (i.e., a single point in time 3 yr following initiation of N additions).

The purpose of this study was to characterize temporal patterns of change in the herbaceous layer of two watersheds of FEF using two temporal scales to assess potential response to experimental additions of N. We examined numerous characteristics of the herb layer, including cover and species diversity, richness, and evenness, because the effects of N has been shown in previous studies to affect various aspects of the plant communities differently (Huberty 1998). The first temporal scale examined inter-annual change over a four-year period (representing 3 to 6 yr following initiation of experimental additions of N) by comparing sampling in July of 1991, 1992, and 1994. The second scale focused on seasonal patterns based on monthly measurements (May through October) of a single year (1994). In particular, we were interested in seeing if there were differences in temporal patterns that could be related to experimental additions of N following 6 yr of treatment.

Materials and Methods. **STUDY SITE.** This study was carried out at the Fernow Experimental Forest (FEF), which occupies ~1900 ha of montane hardwood forests in the Allegheny Mountain section of the unglaciated Allegheny Plateau in Tucker County, north-central West Virginia (39° 03' N, 79° 49' W). Mean annual precipitation is approximately 1430 mm yr⁻¹, with most precipitation occurring between April and September (Gilliam et al. 2001). Two adjacent watersheds were selected for this study. Stands on WS3 were ~25 yr-old at the time of most recent sampling in this study, and are even-aged stands which developed following clear-cutting. WS4 supported uneven-aged stands >90 yr old (Table 1).

Both watersheds support primarily mixed

hardwood stands, with dominant tree species varying with stand age. Early-successional species, such as *Betula lenta* L., *Prunus serotina* Ehrh., and *Liriodendron tulipifera* L. are dominant on WS3, whereas late-successional species, such as *Acer saccharum* Marshall and *Quercus rubra* L., are dominant on WS4.

Soils, similar among study watersheds, 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; Gilliam et al. 1994). Soils of the study watersheds are generally acidic, high in organic matter, and high in cation exchange capacity.

WS3 served as the "treatment" watershed, receiving three aerial applications of $(\text{NH}_4)_2\text{SO}_4$ yr^{-1} , beginning in 1988. March (or sometimes April) and November applications represent approximately 7 kg N ha^{-1} ; July applications are approximately 21 kg N ha^{-1} , for a total of 35 kg N ha^{-1} yr^{-1} . WS4 served as untreated control watershed. Previous studies confirm that these treatments have increased N availability on WS3 relative to WS4, with annual net nitrification averaging 144 and 115 kg N ha^{-1} yr^{-1} , respectively, for the three-year period of 1993 to 1995 (Gilliam et al. 2001). Characteristics for both study watersheds are summarized in Table 1.

FIELD SAMPLING. The herbaceous layer was sampled within seven circular 0.04-ha sample plots in each watershed (representing the full range of elevation and slope aspect) by identifying and visually estimating cover (%) of all vascular plants ≤ 1 m in height within 10 1-m² circular sub-plots in each sample plot, for a total of 140 1-m² sub-plots. Sub-plots were located within sample plots using a stratified-random polar coordinates method (Gaiser 1951), which was employed to avoid over-sampling the center region of circular plots. Sampling was carried out in mid-July of 1991 and 1992. In 1994, plots were sampled monthly from May to October. Nomenclature follows Gleason and Cronquist (1991).

DATA ANALYSIS. The design of this study is an example of simple pseudoreplication, with each watershed representing an experimental condition with a sample size of one (Hurlbert 1984); this is a common statistical problem for field studies carried out at the level of a watershed ecosystem. Accordingly, interpretation of data should be done taking that into account. We

are also aware of the potentially confounding effects of the N treatment with stand age differences. It should be noted, however, that published results of initial sampling of the herb layer shortly after initiation of N additions to WS3 have documented a lack of significant differences between WS3 and WS4 that are related to differences in stand age (Gilliam and Turrill 1993). Thus, it is our contention that any effects that we report are treatment effects, rather than pre-existing differences among watersheds, given the close similarities among watersheds in several "site" variables such as soil texture, soil organic matter, and extractable nutrients (Gilliam et al. 1994).

Data were compared between study watersheds to examine two separate temporal patterns: (1) means for cover (total and selected individual species), species diversity, species richness, and species evenness for one-time sampling of watersheds (in July) in 1991 and 1992 and the July sample from 1994; and (2) monthly means for these same variables over a six-month period in a single growing season. Means were calculated from values of the seven plots for a given sample period. Species diversity of the herbaceous layer was calculated on a per plot basis using the ln-based Shannon index (H') equation. Because H' combines both species richness and evenness, richness and evenness can have varying relationships with H' (Stirling and Wilsey 2001). Accordingly, the Pielou's evenness index (J) was also determined for each plot (Pielou 1966). Relationships between H' and richness versus cover were determined with linear regression (Zar 1996). Means were compared between the two study watersheds using t-tests and among years of sampling with analysis of variance and multiple ranges tests (Zar 1996).

Changes in species composition of the herbaceous layer were analyzed with detrended correspondence analysis (DCA). Inter-annual patterns were assessed by running DCA on 1991, 1992, and July 1994 data combined, followed by calculation of centroids of seven plots per watershed per year. Seasonal patterns were assessed similarly by running DCA on the entire 1994 data set and calculating centroids of clusters of seven sample plots per watershed per month.

Results. INTER-ANNUAL COMPARISONS. There were no significant differences ($P > 0.05$) between watersheds for any sample year for any of the other herb layer characteristics measured,

including herb layer cover, species richness, evenness, and diversity. Cover on WS4, however, decreased significantly ($P < 0.05$) from 1991 to 1992, followed by no change to 1994. By contrast, herb layer cover did not vary significantly across years on WS3 (Fig. 1a).

Species richness varied across sample years similarly between watersheds, with no change from 1991 to 1992, followed by a significant increase to 1994 (Fig. 1b). Species evenness did not vary through time on WS4, but, following no change from 1991 to 1992, increased significantly in 1994 on WS3 (Fig. 1c). Finally, species diversity of the herbaceous layer increased significantly from 1992 to 1994 on WS4, with diversity for 1991 being intermediate between these two extremes. On WS3, diversity did not change from 1991 to 1992, but increased significantly to 1994 (Fig. 1d).

There were few changes in cover of dominant species of the herbaceous layer (Tables 2 and 3). Detrended correspondence analysis (DCA), used to assess annual change in overall species composition of the herbaceous layer of WS3 versus WS4 from 1991 to 1994, confirmed this quantitatively. DCA ordination revealed both a generally close similarity of species composition between WS3 and WS4, as well as minimal change in composition over time for both watersheds (Fig. 2). Based on the location of centroids in ordination space, species composition changed little on WS3 from 1991 to 1992 and much more so from 1992 to 1994. On WS4, change in composition was greater from 1992 to 1994 than it was from 1991 to 1992 (Fig. 2).

SEASONAL PATTERNS. Cover of the herbaceous layer of both watersheds increased from early in the growing season to the middle of the growing season, decreasing thereafter (Fig. 3a). Indeed, there were no significant differences between WS3 and WS4 for any of the monthly cover means in 1994. The same seasonal patterns found for herb layer cover—and lack of significant differences between watersheds—were also evident for species diversity and richness (Figs. 3b, c). By contrast, there was little seasonal change in herb layer species evenness, which was nearly identical between watersheds for all months except October (Fig. 3d).

Monthly mean cover was also calculated for selected dominant species/species groups, including herbaceous plants, such as *Viola* spp. and *Rubus* spp., and seedlings of tree species, such as *Acer pensylvanicum* L. and *Prunus ser-*

otina. Seasonal patterns for *V. rotundifolia* Michx. and *Viola* spp. (a group variously comprising *V. blanda* Willd., *V. canadensis* L., *V. papilionacea* Pursh, *V. pensylvanica* Michx., *V. sagittata* Ait., and *V. sororia* Willd.) were similar between watersheds, although they contrasted with patterns for overall cover (Fig. 3a) in exhibiting a distinct maximum cover in June (Fig. 4). *Rubus* spp. and *A. pensylvanicum* were generally higher in cover on WS3 than on WS4, whereas *P. serotina* was more seasonally dynamic on WS3 than on WS4 (Fig. 4).

Using individual plot values across all monthly sampling periods for each watershed (i.e., combining both spatial and temporal variation), species richness (S) was significantly and linearly related to herb layer cover (C) for both WS3 and WS4 (Fig. 5a). The linear models were nearly identical between watersheds: $S = 6.47 + 0.60C$, $r^2 = 0.58$, $P < 0.0001$ for WS3; $S = 7.12 + 0.59C$, $r^2 = 0.53$, $P < 0.0001$ for WS4. Species diversity (H') was also significantly and linearly related to herb layer cover (C) for both watersheds (Fig. 5b). Models were the following: $H' = 1.47 + 0.051C$, $r^2 = 0.68$, $P < 0.0001$ for WS3; $H' = 1.68 + 0.037C$, $r^2 = 0.29$, $P < 0.0002$ for WS4.

Similar to the analysis of annual change (i.e., Fig. 2), DCA was also used to assess seasonal change in overall species composition of the herbaceous layer of WS3 versus WS4. DCA revealed that, although the herb layer of both watersheds exhibited similar degrees and patterns of seasonal change (i.e., relatively large change from May to June, less change from June to September, and greatest change from September to October), the direction of change contrasted sharply between watersheds in ordination space (Fig. 6).

Discussion. INTER-ANNUAL COMPARISONS. Results of our study, despite being based on more intensive sampling comprising a four-year period, support the findings of earlier studies, which were based on one-time sampling. In particular, there are (1) remarkable similarities between these watersheds that differ greatly in stand age, and (2) negligible responses of the herb layer to the N additions to WS3.

Mean cover for the herb layer did not differ significantly between watersheds (Fig. 1a), averaging 19 and 23 % for WS3 and WS4, respectively. These values are comparable to that found for Hubbard Brook Experimental Forest (24%) (Siccama et al. 1970), greater than the

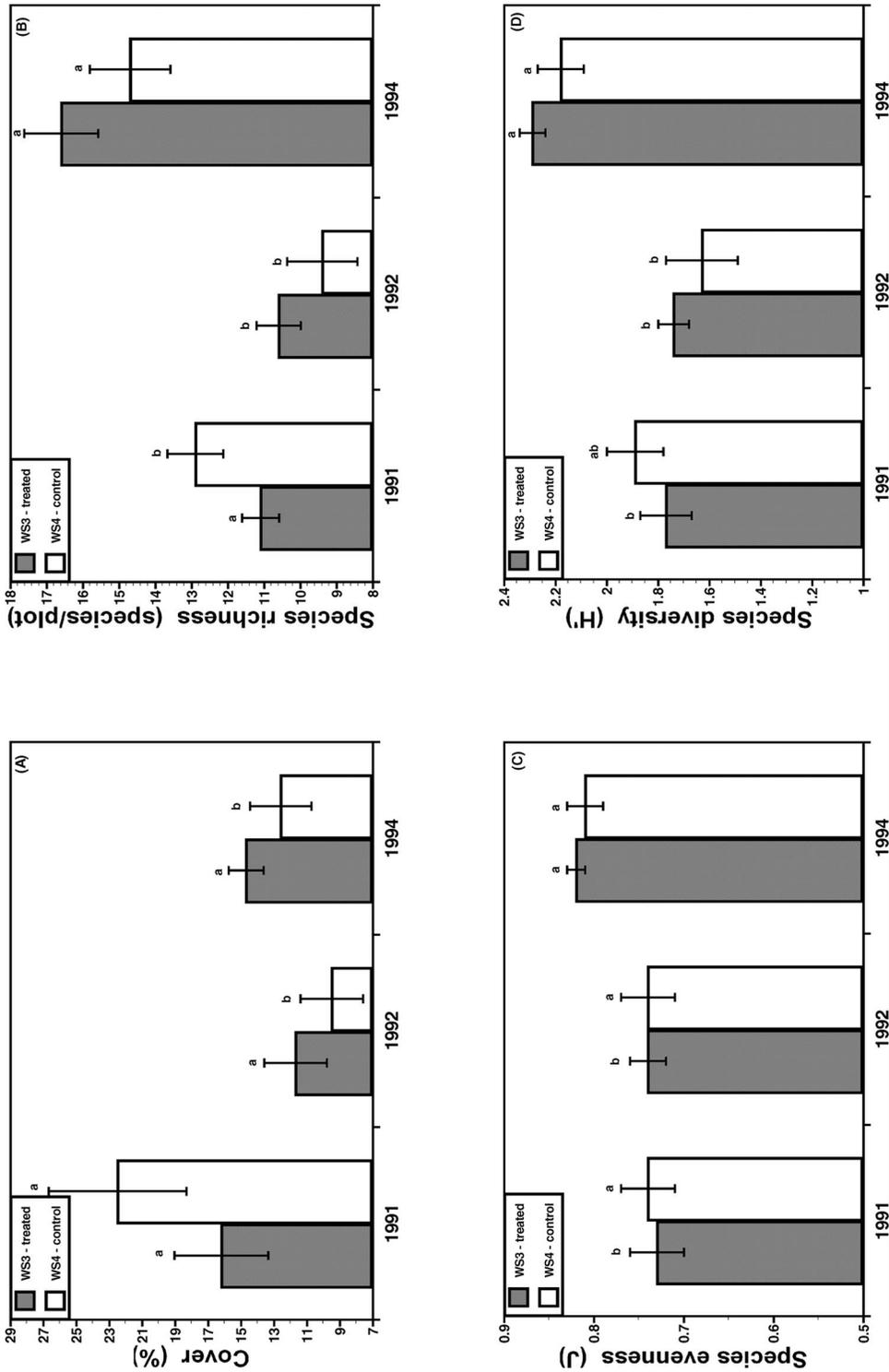


FIG. 1. Mean (\pm SE) cover (A), richness (B), evenness (C), and diversity (D) for the herbaceous layer of WS3 (treatment—shaded bar) and WS4 (control—open bar) of the Fernow Experimental Forest, WV, 1991–1994. Means with the same letter are not significantly different ($P < 0.05$) among years for a given watershed. Means were not significantly different ($P < 0.05$) between watersheds for any variable or year.

Table 2. Herbaceous layer species on WS3. Values shown are importance values based on relative cover.

1991		1992		1994	
Species	IV	Species	IV	Species	IV
<i>Viola</i> spp.	23.7	<i>Viola</i> spp.	26.0	<i>Viola</i> spp.	23.9
<i>Smilax rotundifolia</i>	19.1	<i>Smilax rotundifolia</i>	21.6	<i>Smilax rotundifolia</i>	20.6
<i>Lycopodium flabelliforme</i>	15.9	<i>Acer pensylvanicum</i>	12.8	<i>Rubus</i> spp.	13.4
<i>Acer pensylvanicum</i>	12.9	<i>Lycopodium flabelliforme</i>	10.6	<i>Acer pensylvanicum</i>	12.7
<i>Sassafras albidum</i>	10.0	<i>Rubus</i> spp.	9.9	<i>Sassafras albidum</i>	6.9
<i>Rubus</i> spp.	4.4	<i>Sassafras albidum</i>	8.0	<i>Prunus serotina</i>	6.8
<i>Prunus serotina</i>	3.1	<i>Prunus serotina</i>	2.9	<i>Lycopodium flabelliforme</i>	3.5
<i>Polygonum bistorta</i>	2.3	<i>Polygonum bistorta</i>	2.1	<i>Dryopteris marginalis</i>	2.6
<i>Dryopteris marginalis</i>	1.6	<i>Fagus grandifolia</i>	1.4	<i>Diospyros virginiana</i>	1.9
<i>Fagus grandifolia</i>	1.5	<i>Thelypteris noveboracensis</i>	1.0	<i>Quercus rubra</i>	1.0
<i>Polysticum acrostichoides</i>	1.5	<i>Dryopteris marginalis</i>	0.6	<i>Medeola virginiana</i>	0.9
<i>A. saccharum</i>	1.4	<i>Magnolia acuminata</i>	0.6	<i>Panicum</i> spp.	0.8
<i>Dioscorea quaternata</i>	0.7	<i>A. saccharum</i>	0.5	<i>Carex</i> spp.	0.8
<i>Fraxinus americana</i>	0.4	<i>Panicum</i> spp.	0.4	<i>Aster</i> spp.	0.7
<i>Panicum</i> spp.	0.4	<i>Boehmeria cylindrica</i>	0.4	<i>Magnolia acuminata</i>	0.7
<i>Uvularia perfoliata</i>	0.4	<i>Robinia pseudoacacia</i>	0.4	<i>Acer rubrum</i>	0.6
<i>Carya</i> spp.	0.3	<i>Uvularia sessilifolia</i>	0.3	<i>A. saccharum</i>	0.4
<i>Magnolia acuminata</i>	0.2	<i>A. rubrum</i>	0.1	<i>Fragaria</i> spp.	0.3
<i>Laportea canadensis</i>	0.1	<i>Liriodendron tulipifera</i>	0.1	<i>Robinia pseudoacacia</i>	0.3
<i>Cimicifuga racemosa</i>	0.1	<i>Quercus rubra</i>	0.1	<i>Uvularia perfoliata</i>	0.3
		<i>Fraxinus americana</i>	0.1	<i>Osmorhiza claytonii</i>	0.3
				<i>Arisaema triphyllum</i>	0.3
				<i>Solidago caesia</i>	0.2
				<i>Betula lenta</i>	0.1
				<i>Liriodendron tulipifera</i>	0.1

Table 3. Herbaceous layer species on WS4. Values shown are importance values based on relative cover.

1991		1992		1994	
Species	IV	Species	IV	Species	IV
<i>Laportea canadensis</i>	16.4	<i>Laportea canadensis</i>	16.9	<i>Viola</i> spp.	28.2
<i>Viola</i> spp.	14.1	<i>Viola</i> spp.	15.4	<i>Laportea canadensis</i>	13.2
<i>Acer pensylvanicum</i>	10.8	<i>Smilax rotundifolia</i>	10.2	<i>Smilax rotundifolia</i>	10.8
<i>Vaccinium vacillans</i>	9.3	<i>Acer pensylvanicum</i>	10.1	<i>Rubus</i> spp.	8.2
<i>Rubus</i> spp.	9.0	<i>Prunus serotina</i>	9.8	<i>Acer pensylvanicum</i>	7.7
<i>A. saccharum</i>	8.3	<i>Rubus</i> spp.	8.5	<i>Prunus serotina</i>	6.5
<i>Prunus serotina</i>	5.6	<i>Vaccinium vacillans</i>	8.1	<i>A. saccharum</i>	4.3
<i>Dryopteris marginalis</i>	5.1	<i>Polysticum acrostichoides</i>	6.7	<i>Vaccinium vacillans</i>	3.9
<i>Smilax rotundifolia</i>	4.5	<i>A. saccharum</i>	2.8	<i>Polysticum acrostichoides</i>	3.2
<i>Polysticum acrostichoides</i>	3.7	<i>Cardamine angustata</i>	2.6	<i>Dryopteris marginalis</i>	2.9
<i>Polygonum bistorta</i>	3.2	<i>Carpinus caroliniana</i>	2.2	<i>Castanea dentata</i>	1.7
<i>Ambrosia artemisiifolia</i>	1.8	<i>Dryopteris marginalis</i>	2.1	<i>Diospyros virginiana</i>	1.6
<i>Quercus rubra</i>	1.6	<i>Polygonum bistorta</i>	1.1	<i>Arisaema triphyllum</i>	1.4
<i>Dioscorea quaternata</i>	1.2	<i>Fraxinus americana</i>	0.7	<i>Quercus rubra</i>	1.2
<i>Castanea dentata</i>	1.1	<i>Fagus grandifolia</i>	0.6	<i>Fraxinus americana</i>	1.0
<i>Brachyelytrum erectum</i>	1.0	<i>Thelypteris noveboracensis</i>	0.6	<i>Magnolia acuminata</i>	0.7
<i>Fagus grandifolia</i>	1.0	<i>Stellaria media</i>	0.5	<i>Tovaria virginiana</i>	0.7
<i>Fraxinus americana</i>	0.9	<i>Uvularia sessilifolia</i>	0.3	<i>Fagus grandifolia</i>	0.6
<i>Liriodendron tulipifera</i>	0.3	<i>Cimicifuga racemosa</i>	0.2	<i>Caulophyllum thalictroides</i>	0.5
<i>Cimicifuga racemosa</i>	0.3	<i>Magnolia acuminata</i>	0.2	<i>Medeola virginiana</i>	0.3
<i>Carya</i> spp.	0.3	<i>Medeola virginiana</i>	0.2	<i>Sassafras albidum</i>	0.3
<i>Magnolia acuminata</i>	0.3	<i>Quercus rubra</i>	0.2	<i>Carex</i> spp.	0.3
<i>Nyssa sylvatica</i>	0.1	<i>Sassafras albidum</i>	0.2	<i>Liriodendron tulipifera</i>	0.3
<i>Uvularia perfoliata</i>	0.1	<i>Stellaria pubera</i>	0.2	<i>Aster</i> spp.	0.1
<i>Sassafras albidum</i>	0.1			<i>Betula lenta</i>	0.1
				<i>Uvularia perfoliata</i>	0.1

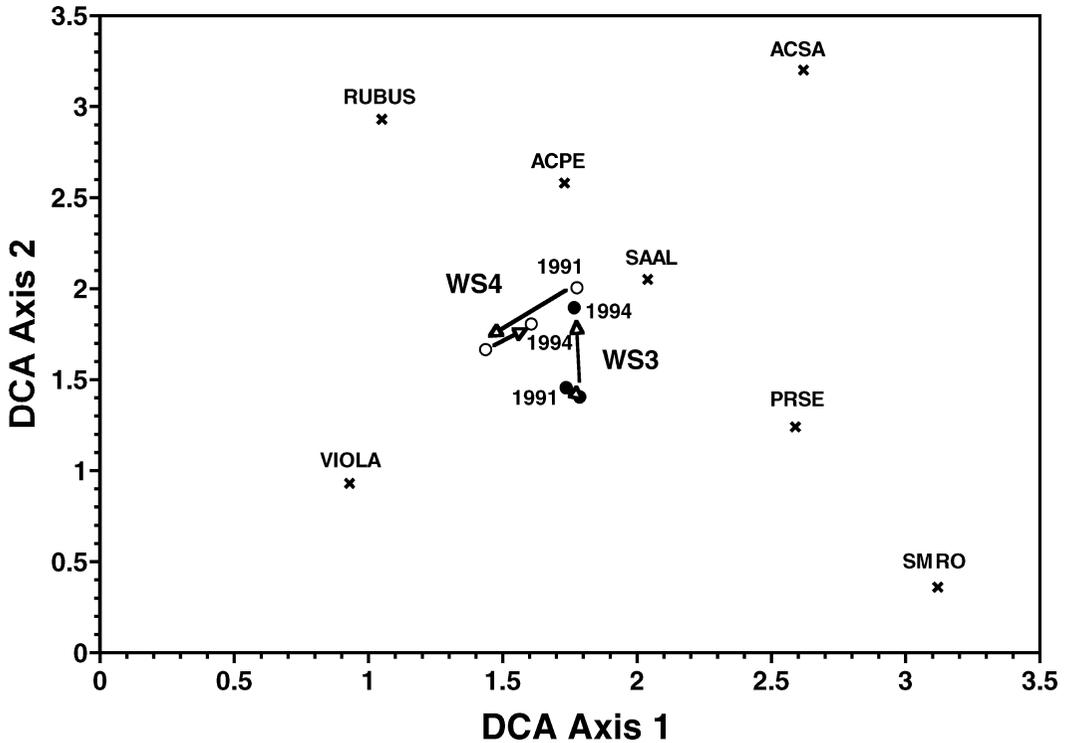


FIG. 2. Detrended correspondence analysis of species composition of the herbaceous layer of WS3 (treatment—solid symbol) and WS4 (control—open symbol) of the Fernow Experimental Forest, WV, 1991–1994. Each point shown represents a centroid of seven sample plots per watershed per year. Centroids are connected to depict trajectory of change in composition from 1991 to 1992 and 1992 to 1994. Location in ordination space is shown for prominent herb layer species: ACPE = *Acer pensylvanicum*; ACSA = *Acer saccharum*; VIOLA = *Viola* spp.; PRSE = *Prunus serotina*; RUBUS = *Rubus* spp.; SAAL = *Sassafras albidum*; SMRO = *Smilax rotundifolia*.

10% found for an Appalachia oak forest by McEvoy et al. (1980) and the 16% of unburned loblolly pine forests (Gilliam and Christensen 1986), and less than the 31% for a New Jersey hardwood forest (Davison and Forman 1970). The lack of a stand age effect on herb layer cover at FEF supports the conclusion of Gilliam (2002) that the herbaceous layer appears to recover and reestablish rapidly following disturbance in these forest ecosystems.

The significant increase in species diversity from 1991 and 1992 to 1994 (Fig. 1d) appears to have arisen from simultaneous increases in numbers of species on a plot basis (S; species richness) and in equitability of dominance among herb layer species (J; species evenness) (Fig. 1b, c). It would be little beyond pure speculation to explain this change, but it could have resulted from changes in meteorological conditions, particularly soil moisture availability early in the growing season. Archived data from the National Weather Service for Tucker County, West

Virginia, (<http://www.ncdc.noaa.gov/oa/climate/research/cag3/wv.html>) indicate little variation in both annual mean temperatures and mean monthly temperatures from 1991 to 1994. By contrast, total precipitation was higher in 1994 than in the other years, and was especially higher in mid to late spring. The lack of significant difference between watersheds for any given year is consistent with the results for similar mixed hardwood stands of West Virginia by Ford et al. (2000), who found that species diversity, richness, and evenness did not vary significantly among stands of ages 15, 25, 50, and ≥ 85 years.

DCA directly assesses β diversity, in this case between watersheds and among years, with species turnover (i.e., complete change in species composition) occurring for every “unit” (SD; average standard deviation of species turnover) (Gauch 1982). Variation among watershed-year centroids was approximately 0.4 along DCA axis 1 and approximately 0.6 along DCA axis 2 (Fig. 2). Thus, we can conclude that species

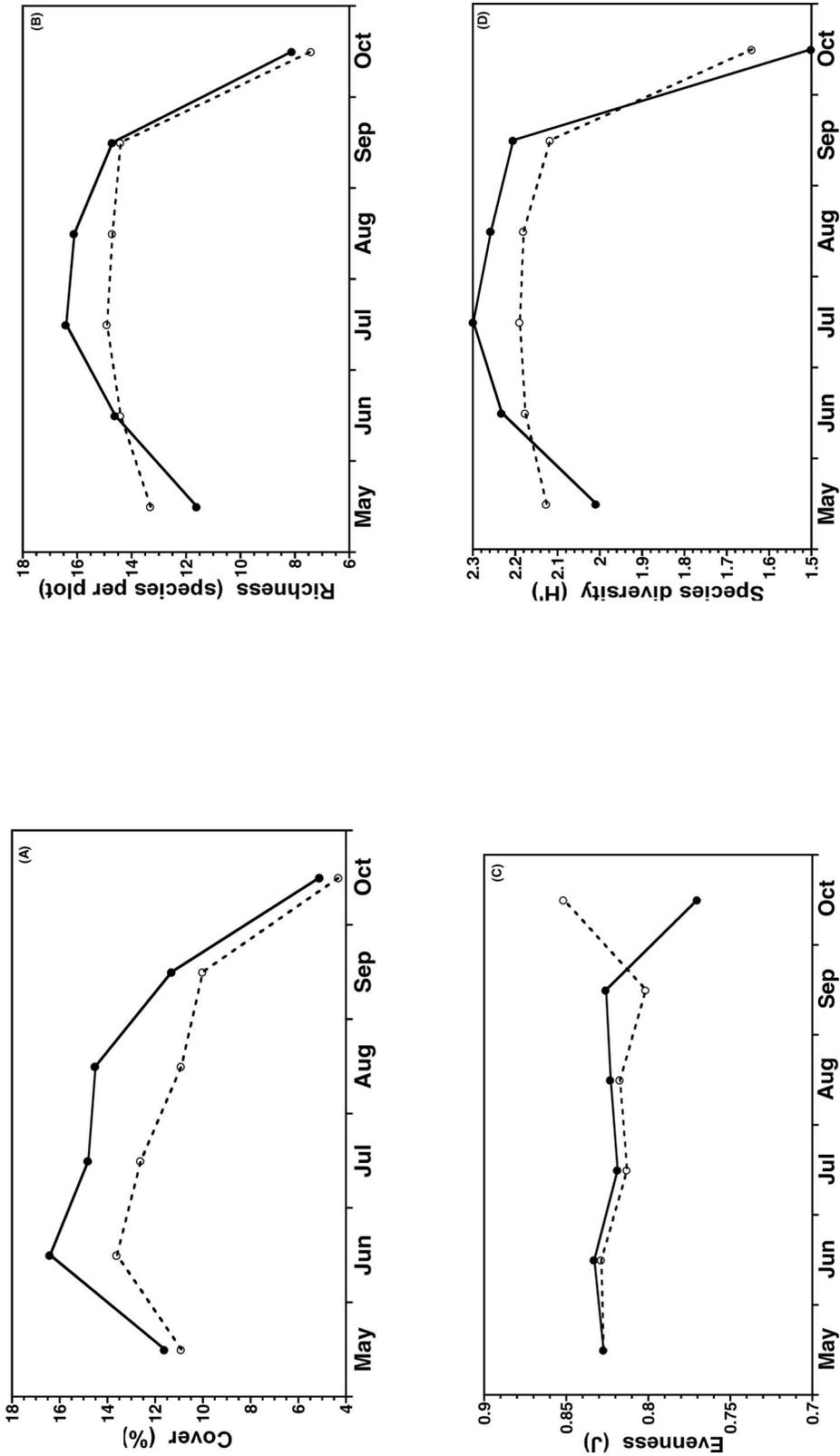


FIG. 3. Mean monthly cover (A), richness (B), evenness (C), and diversity (D) for the herbaceous layer of WS3 (treatment—solid symbol and line) and WS4 (control—open symbol, dashed line) of the Fernow Experimental Forest, WV, sampled in 1994. Means were not significantly different ($P < 0.05$) between watersheds for any variable or month.

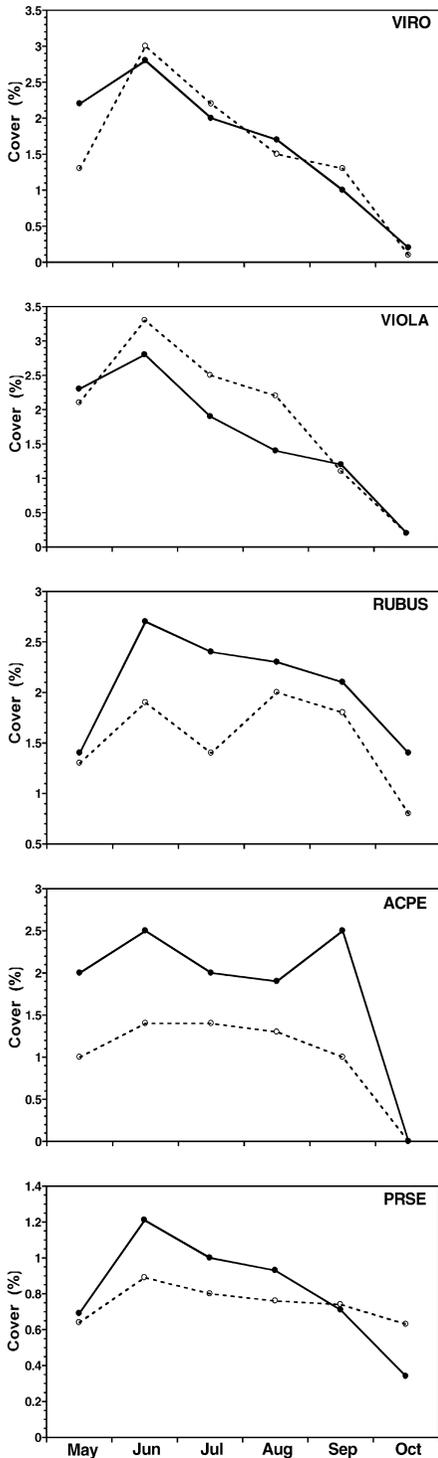


FIG. 4. Mean monthly cover of individual species of the herbaceous layer of WS3 (treatment—solid symbol and line) and WS4 (control—open symbol, dashed line) of the Fernow Experimental Forest, WV, sampled in 1994: VIRO = *Viola rotundifolia*; VIOLA = *Viola* spp.; RUBUS = *Rubus* spp.; ACPE = *Acer pensylvanicum*; PRSE = *Prunus serotina*.

composition did not vary appreciably between watersheds for any year; neither did it vary appreciably among years for either watershed. This conclusion is supported by the general similarities in cover values for dominant herb layer species between watersheds (Tables 2 and 3).

SEASONAL PATTERNS. Seasonal patterns of herb layer cover were both predictable (low early in the growing season, increasing during growing season, declining toward dormant season) and quite similar between two watersheds that differ greatly in stand age. Such similarities confirm the significance of slope aspect (via light and moisture regimes) in affecting the herb layer, as has been found in other studies (e.g., Goebel et al. 1999, McCarthy 2003), considering that WS3 and WS4 are both of a southern aspect (Table 1). In other words, the lack of differences in cover between watersheds both over time (Fig. 1a) and seasonally (Fig. 3a), despite that WS3 was (1) clearcut in 1969 and (2) receives N additions, may come from the strong influence that slope and aspect have on herb layer dynamics.

Similarities in seasonal patterns for cover and richness (Figs. 3a, b), and the significant relationship between herb layer cover and richness (Fig. 5a) suggest that seasonal increases and decreases in herb layer cover were brought about by appearance and disappearance, respectively, of species of different phenologies (Goebel et al. 1999, Small and McCarthy 2002). For example, the May to June increase of an average ~6% (Fig. 3a) was largely the result of an increase of an average of 3 species per plot (Fig. 3b), rather than simply increased growth of the species already present on the plots, confirming conclusions of Gilliam (2002).

Casado et al. (2004) found a significant linear and positive relationship between cover and richness of herbaceous species in Mediterranean-type shrubland ecosystems of the Iberian Peninsula. They did not examine relationships between diversity and cover, as we did, but concluded that richness—cover relationships can be scale-dependent (Casado et al. 2004). Similarities between richness versus cover and diversity versus cover in our data (Figures 5a and 5b), suggest that the number of species (richness), rather than the equitability of species (evenness), determines species diversity for the herb layer at FEF. Certainly, species evenness displayed minimal seasonal change in the herb layer of both watersheds (Fig. 3d), in contrast to pro-

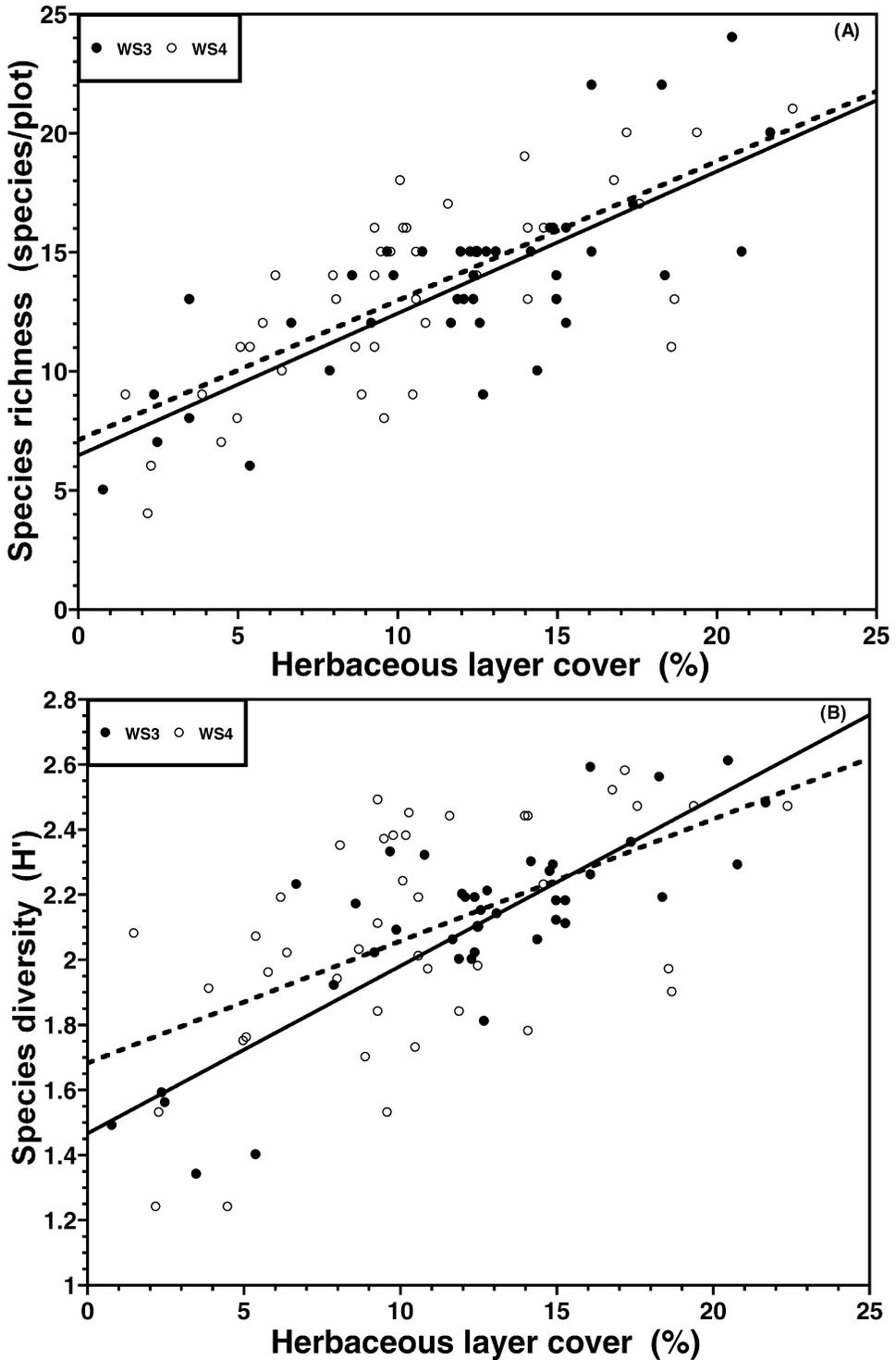


FIG. 5. Relationship between species richness (A) and species diversity (B) versus cover for the herbaceous layer of WS3 (treatment—solid symbol and line) and WS4 (control—open symbol, dashed line) of the Fernow Experimental Forest, WV, sampled in 1994. Each point represent a single sample plot (seven plots per watershed per month) for all months combined. For species richness (S) versus cover (C): $S = 6.47 + 0.60 C$, $r^2 = 0.58$, $P < 0.0001$ for WS3; $S = 7.12 + 0.59 C$, $r^2 = 0.53$, $P < 0.0001$ for WS4. For species diversity (H') versus cover: $H' = 1.47 + 0.051 C$, $r^2 = 0.68$, $P < 0.0001$ for WS3; $H' = 1.68 + 0.037 C$, $r^2 = 0.29$, $P < 0.0002$ for WS4.

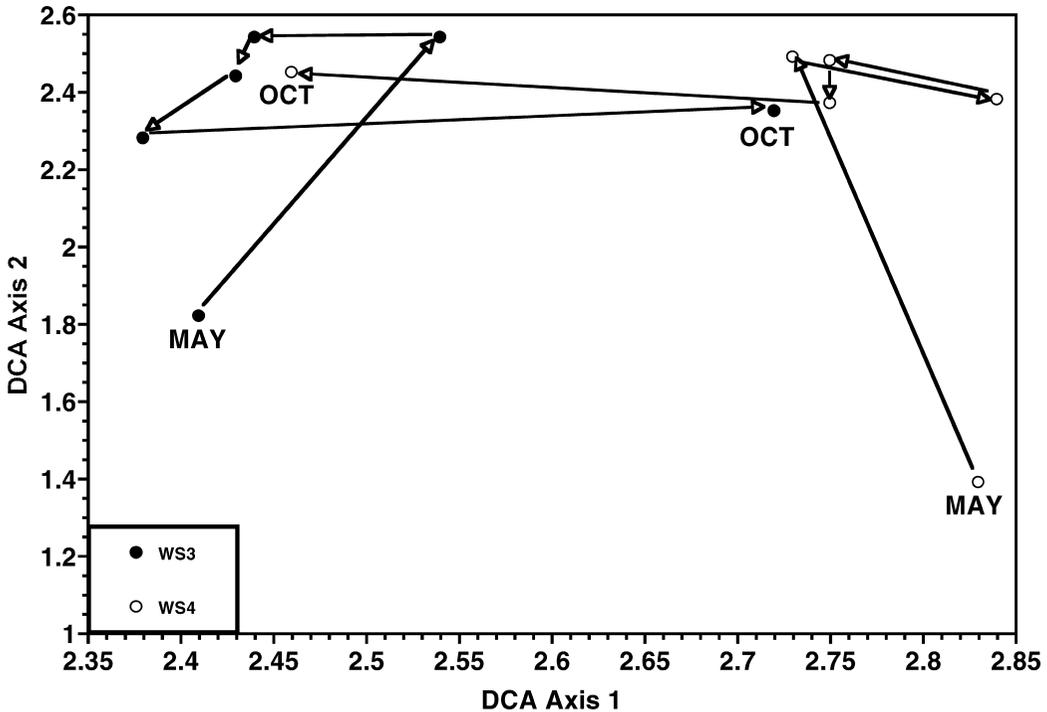


FIG. 6. Detrended correspondence analysis of species composition of the herbaceous layer of WS3 (treatment—closed symbols) and WS4 (control—open symbols) of the Fernow Experimental Forest, WV, 1994. Each point shown represents a centroid of seven sample plots per watershed per month. Centroids are connected to depict trajectories of change in species composition of the herb layer from May to October.

nounced changes in seasonal patterns for species richness and diversity (Fig. 3b and c). Our findings regarding these relationships may have resulted, at least in part, from the number of herb layer species characteristic for mixed mesophytic forests, such as those found at FEF. For example, Stirling and Wilsey (2001) found that richness and diversity were weakly correlated for sites with low numbers of species (≤ 10 species), not correlated for sites with high numbers of species (≥ 100), but highly correlated for sites with intermediate numbers of species (> 10 and < 100).

Seasonal patterns for individual species/species groups were also generally similar between treatment and control watersheds. This was especially the case for *Viola rotundifolia* and the *Viola* spp. group as a whole (Fig. 4). These similarities suggest that the *Viola* species found at FEF are adapted to a wide range of environmental conditions. Indeed, studies have demonstrated considerable variability within and among species of *Viola* in terms of reproduction (Griffith 1998, Culley 2002) and growth (Curtis and Kincaid 1984). Some species are capable of producing both chasmogamous and cleistoga-

mous flowers (Culley 2002), and many combine sexual reproduction via prolific flower production with asexual reproduction via stolons and rhizomes (Griffith 1998). The species found in our study (*V. blanda*, *V. canadensis* L., *V. papilionacea*, *V. pensylvanica*, *V. rotundifolia*, *V. sagittata*, and *V. sororia*) are all widely distributed in forests of the eastern United States, further suggesting adaptations to widely varying environments (Gleason and Cronquist 1991), including variation in light and soil nutrient availability (Curtis and Kincaid 1984, Griffith 1998). Rankin and Tramer (2002) found *V. blanda* to be a prominent component of the herb layer in hardwood stands both 0–5 yr and 65 yr following harvesting, and to have equally high cover in both canopy gaps and intact hardwood canopy. Similarly, Ruben et al. (1999), comparing herb layer composition 25 and 60 yr post harvest in northern hardwood forests, classified *V. rotundifolia* as an insensitive species in response to harvest-mediated disturbance. They found it to be of high relative cover in harvested plots independent of stand age (Ruben et al. 1999).

Also notable among herb layer species compared between watersheds is *Rubus* spp., which

was generally higher on WS3 than on WS4 (Fig. 4). This difference, although not large overall, maybe related to successional age of the two watersheds (Table 1), considering that *Rubus* spp. represents a group of disturbance-maintained species (Roberts and Dong 1993). Kochenderfer and Wendel (1983) found substantial change in composition and dominance of the herb layer immediately following harvest on WS3 in 1969. *Rubus* spp. increased from approximately 20% of herb cover in year 1 following harvesting to just under 40% by year 5, declining sharply by year 10 (Kochenderfer and Wendel 1983). Annual mean cover for *Rubus* spp. was approximately 1–2.5% for both WS3 and WS4 during the period of this study (1991–1994), indicating that cover has remained low since last reported by Kochenderfer and Wendel (1983).

Multivariate analysis of the seasonal herb layer data (Fig. 6) support conclusions based on empirical data on cover, richness, and diversity (Fig. 3a, b, c). That is, there was greater change from May to June and September to October than during the period June to September. However, as with the results of DCA for inter-annual comparisons (Fig. 2), the gradient lengths were generally short along both axes, suggesting that the relative amount change in species composition was small for both watersheds.

INFLUENCE OF STAND DEVELOPMENT AND N-DEPOSITION. The lack of significant differences in herb layer characteristics between watersheds at the beginning of our sampling period (i.e., 1991) both supports, not surprisingly, conclusions of previous studies (e.g., Gilliam and Turrill 1993) and provides a baseline for further evaluation of effects of N additions on the herb layer of WS3. This lack of difference is relevant to the on-going debate regarding the response of the herbaceous layer of forest ecosystems to disturbances (see Battles et al. 2001, Roberts and Gilliam 2003, and Roberts 2004 for recent reviews). Natural disturbances, such canopy gap formation, increase in frequency during secondary succession in ways that can influence herb layer dynamics (Goldblum 1997, Schumann et al. 2003). Reader and Bricker (1992) found herb layer species of a deciduous forest in southern Ontario to be sensitive to gap size. However, forest management includes treatments that represent a gradient of disturbance intensity (Gilliam and Roberts 1995), virtually all of which are greater than that of gap formation. The more intensive practices are related to plantation for-

estry, often coupled with thinning and fertilization (Thomas et al. 1999, Ramovs and Roberts 2003).

A potentially important variable influencing herb layer dynamics is light. Although light penetration to the forest floor is generally assumed to decrease linearly with stand age, Neufeld and Young (2003) demonstrated that this is most often not the case. Indeed, Brown and Parker (1994) measured transmittance of light (as photon flux density; PFD) in hardwood stands ranging from 10 to >340 yr old. They found no differences in percent PFD between stand ages represented by WS3 and WS4 used in this study, 25 and ~100 yr, respectively. Thus, we feel that light, though not measured here, plays a minimal role in determining variation in herb layer dynamics in this study.

Although response of the herb layer to harvesting is typically rapid, with an early dominance of disturbance-maintained species (Roberts and Zhu 2002), several studies have demonstrated that herb layer recovery following disturbance can occur in a little as 20–30 years (Reiners 1992, Olivero and Hix 1998, Frederickson et al. 1999, Ford et al. 2000). Halpern and Spies (1995) found that changes in herb 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 yr). Because hardwood stands on WS3 fall within these ranges of time, it is likely that the lack of significant differences in herb layer composition, cover, and diversity between WS4 and WS3—especially for 1991 and 1992—resulted from similar rapid recovery of the herb layer on WS3 by 20 years following clearcutting.

The lack response of the herbaceous layer to the addition of 35 kg N ha⁻¹ yr⁻¹, which had been carried out for 6 yr by the time of the 1994 sampling, is particularly notable in its sharp contrast to results of other studies that showed more sensitive responses of herb layer species to experimental additions of N. Hurd et al. (1998) found that cover of prominent herb species in hardwood forests of the Adirondack Mountains declined significantly after only 3 yr of treatment with (NH₄)₂SO₄ at rates of 14 and 28 kg N ha⁻¹ yr⁻¹. This decline was accompanied by increases in relative cover of fern species, suggesting that some of the decline in herb cover may have resulted from increased shading by the ferns, which have been shown to reduce midsummer

light levels by as much as 70% (George and Bazzaz 2003). Working in Harvard Forest, Rainey et al. (1999) reported declines in density and biomass of herb layer species of 80% and ~90%, respectively, after 7 yr of additions of NH_4NO_3 at rates of 50 and 150 kg N ha^{-1} yr^{-1} . Strengbom et al. (2003) conducted a synoptic survey of 557 Swedish conifer stands and concluded that even low rates of enhanced N deposition can alter herb layer species. Strengbom et al. (2001) found that the effects of increased N deposition on the herb layer of managed Swedish forests can be long-lived. Such effects, including declines in ericaceous species and increases in nitrophilous grasses, remained as long as 30 yr after cessation of treatments with N fertilizers.

We suggest that the lack of measurable response of the herbaceous layer to 6 yr of aerial applications of 35 kg N ha^{-1} yr^{-1} to WS3 resulted from two factors: (1) high ambient atmospheric deposition of N and (2) N saturation status. Wet deposition of N ($\text{NH}_4\text{-N} + \text{NO}_3\text{-N}$) averages ~10 kg N ha^{-1} yr^{-1} at FEF, is even higher at higher elevations, and increases markedly during the growing season (Gilliam et al. 2001). Thus, the N addition to WS3 represents a lower relative addition than it would at a site with lower ambient inputs of N. This is consistent with results of Hurd et al. (1998), who found that plant responses to N additions to hardwood forests of the Adirondack Mountains was greatest at sites with low atmospheric inputs of N.

Several watersheds of FEF, including WS3 and WS4, are well-documented to be N saturated (Peterjohn et al. 1996, Gilliam et al. 2004). Gilliam et al. (2001) found rates of net N mineralization and nitrification for untreated watersheds (including WS4) to be ~125 and ~114 kg N ha^{-1} yr^{-1} , respectively; for WS3 this was 135 and 141 kg N ha^{-1} yr^{-1} . Thus, the aerial application of N in this study is only an increase in available N of 25% relative to the amount that is generated by net N mineralization. It is likely, then, that the N treatment on WS3 represents a comparatively small addition of an essential nutrient that is no longer growth-limiting. Future work at FEF will include repeated sampling of these plots, using data summarized in this paper as baseline for further analysis.

Literature Cited

- BATTLES, J. J., A. J. SHLISKY, R. H. BARRETT, R. C. HEALD, AND B. H. ALLEN-DIAZ. 2001. The effects

of forest management on plant species diversity in a Sierran conifer forest. *For. Ecol. Manage.* 146: 211–222.

- BOBBINK, R., M. HORNUNG, AND J. G. M. ROELOFS. 1998. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *J. Ecol.* 86: 717–738.
- BROWN, M. J. AND G. G. PARKER. 1994. Canopy light transmittance in a chronosequence of mixed-species deciduous forests. *Can. J. For. Res.* 24: 1694–1703.
- CASADO, M. M., I. CASTRO, L. RAMIREZ-SANZ, M. COSTA-TENORIO, M. DE MIGUEL, AND F. D. PINEDA. 2004. Herbaceous plant richness and vegetation cover in Mediterranean grasslands and shrubs. *Plant Ecol.* 170: 83–91.
- CHRISTENSEN, N. L. AND F. S. GILLIAM. 2003. Temporal and spatial patterns of herbaceous layer communities on the North Carolina Piedmont, p. 224–237. *In* F. S. Gilliam and M. R. Roberts [eds.], *The Herbaceous Layer in Forests of Eastern North America*, Oxford University Press, New York, NY.
- CULLEY, T. M. 2002. Reproductive biology and delayed selfing in *Viola pubescens* (Violaceae), an understory herb with chasmogamous and cleistogamous flowers. *Int. J. Plant Sci.* 163: 113–122.
- CURTIS, W. F. AND D. T. KINCAID. 1984. Leaf conductance responses of *Viola* species from sun and shade habitats. *Can. J. Bot.* 62: 1268–1272.
- DAVISON, S. E. AND R. T. T. FORMAN. 1970. Herb and shrub dynamics in a mature oak forest: a thirty-year study. *Bull. Torrey Bot. Club* 109: 64–73.
- FORD, W. M., R. H. ODOM, P. E. HALE, AND B. R. CHAPMAN. 2000. Stand-age, stand characteristics, and landform effects on understory herbaceous communities in southern Appalachian cove-hardwoods. *Biol. Conserv.* 93: 237–246.
- FREDERICKSEN, T. S., B. D. ROSS, W. HOFFMAN, M. L. MORRISON, J. BEYEA, B. N. JOHNSON, M. B. LESTER, AND E. ROSS. 1999. Short-term understory plant community responses to timber-harvesting intensity on non-industrial forestlands in Pennsylvania. *For. Ecol. Manage.* 116: 129–139.
- GAISER, R. N. 1951. Random sampling within circular plots by means of polar coordinates. *J. For.* 49: 916–917.
- GAUCH, H. G. 1982. *Multivariate analysis in community ecology*. Cambridge University Press, Cambridge.
- GEORGE, L. O. AND F. A. BAZZAZ. 2003. The herbaceous layer as a filter determining spatial pattern in forest tree regeneration, p. 265–282. *In* F. S. Gilliam and M. R. Roberts [eds.], *The Herbaceous Layer in Forests of Eastern North America*, Oxford University Press, New York, NY.
- GILLIAM, F. S. 2002. Effects of harvesting on herbaceous layer diversity of a central Appalachian hardwood forest. *For. Ecol. Manage.* 155: 33–43.
- GILLIAM, F. S. AND N. L. CHRISTENSEN. 1986. Herb-layer response to burning in pine flatwoods of the lower Coastal Plain of South Carolina. *Bull. Torrey Bot. Club* 113: 42–45.
- GILLIAM, F. S. AND M. R. ROBERTS. 1995. Impacts of forest management on plant diversity. *Ecol. Appl.* 5: 911–912.
- GILLIAM, F. S. AND M. R. ROBERTS. 2003. Introduction: conceptual framework for studies of the herbaceous

- layer, p. 3–11. *In* F. S. Gilliam and M. R. Roberts [eds.], *The Herbaceous Layer in Forests of Eastern North America*, Oxford University Press, New York, NY.
- GILLIAM, F. S. AND N. L. TURRILL. 1993. Herbaceous layer cover and biomass in a young versus a mature stand of a central Appalachian hardwood forest. *Bull. Torrey Bot. Club* 120: 445–450.
- GILLIAM, F. S., B. M. YURISH, AND M. B. ADAMS. 2001. Temporal and spatial variation of nitrogen transformations in nitrogen-saturated soils of a Central Appalachian hardwood forest. *Can. J. For. Res.* 31: 1768–1785.
- GILLIAM, F. S., M. B. ADAMS, D. A. DICK, AND M. L. KERR. 2004. Effects of silvicultural practices on soil carbon and nitrogen in a nitrogen saturated Central Appalachian hardwood forest ecosystem. *Environ. Manage.* 33: S108–S119.
- GILLIAM, F. S., N. L. TURRILL, S. D. AULICK, D. K. EVANS, AND M. B. ADAMS. 1994. Herbaceous layer and soil response to experimental acidification in a central Appalachian hardwood forest. *J. Env. Qual.* 23: 835–844.
- GLEASON, H. A. AND A. CRONQUIST. 1991. *Manual of Vascular Plants of the Northeastern United States and Adjacent Canada*, 2nd ed. New York Botanical Garden, New York, NY.
- GOEBEL, P. C., D. M. HIX, AND A. M. OLIVERO. 1999. Seasonal ground-flora patterns and site factor relationships of second-growth and old-growth south-facing forest ecosystems, southeastern Ohio, USA. *Nat. Areas J.* 19: 12–19.
- GOLDBLUM, D. 1997. The effects of treefall gaps on understory vegetation in New York, USA. *J. Veg. Sci.* 8: 125–132.
- GRIFFITH, C. JR. 1998. The response of *Viola blanda* Willd. (Violaceae) to phosphorus fertilization and shading. *J. Torrey Bot. Soc.* 125: 194–198.
- HALPERN, C. B. AND T. A. SPIES. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. *Ecol. Appl.* 5: 913–934.
- HUBERTY, L. E., K. L. GROSS, AND C. J. MILLER. 1998. Effects of nitrogen addition on successional dynamics and species diversity in Michigan old-fields. *J. Ecol.* 86: 794–803.
- HURD, T. M., A. R. BRACH, AND D. J. RAYNAL. 1998. Response of understory vegetation of Adirondack forests to nitrogen additions. *Can. J. For. Res.* 28: 799–807.
- HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54: 187–211.
- KOCHENDERFER, J. N. AND G. W. WENDEL. 1983. Plant succession and hydrologic recovery on a deforested and herbicided watershed. *For. Sci.* 29: 545–558.
- MCCARTHY, B. C. 2003. The herbaceous layer of eastern old-growth deciduous forests, p. 163–176. *In* F.S. Gilliam and M.R. Roberts [eds.], *The Herbaceous Layer in Forests of Eastern North America*, Oxford University Press, New York, NY.
- MCEVOY, T. J., T. L. SHARIK, AND D. W. SMITH. 1980. Vegetative structure of an Appalachian oak forest in southwestern Virginia. *Amer. Midl. Nat.* 103: 96–105.
- MULLER, R. N. 2003. Nutrient relations of the herbaceous layer in deciduous forest ecosystems, p. 15–37. *In* F.S. Gilliam and M.R. Roberts [eds.], *The Herbaceous Layer in Forests of Eastern North America*, Oxford University Press, New York, NY.
- NEUFELD, H. S. AND D. R. YOUNG. 2003. Ecophysiology of the herbaceous layer in temperate deciduous forests, p. 38–90. *In* F.S. Gilliam and M.R. Roberts [eds.], *The Herbaceous Layer in Forests of Eastern North America*, Oxford University Press, New York, NY.
- OLIVERO, A. M. AND D. M. HIX. 1998. Influence of aspect and stand age on ground flora of southeastern Ohio forest ecosystems. *Plant Ecol.* 139: 177–187.
- PETERJOHN, W. T., M. B. ADAMS, AND F. S. GILLIAM. 1996. Symptoms of nitrogen saturation in two central Appalachian hardwood forests. *Biogeochem.* 35: 507–522.
- PIELOU, E. C. 1966. The measurement of diversity in different types of biological collections. *J. Theor. Biol.* 13: 131–144.
- PREGITZER, K. S. AND B. V. BARNES. 1982. The use of ground flora to indicate edaphic factors in upland ecosystems of the McCormick Experimental Forest, Upper Michigan. *Can. J. For. Res.* 12: 661–672.
- RAINEY, S. M., K. J. NADELHOFFER, W. L. SILVER, AND M. R. DOWNS. 1999. Effects of chronic nitrogen additions on understory species in a red pine plantation. *Ecol. Appl.* 9: 949–957.
- RAMOV, B. V. AND M. R. ROBERTS. 2003. Understory vegetation and environment responses to tillage, forest harvesting, and conifer plantation development. *Ecol. Appl.* 13: 1682–1700.
- RANKIN, W. T. AND E. J. TRAMER. 2002. Understory succession and the gap regeneration cycle in a *Tsuga canadensis* forest. *Can. J. For. Res.* 32: 16–23.
- READER, R. J. AND B. D. BRICKER. 1992. Response of five deciduous forest herbs to partial canopy removal and patch size. *Am. Midl. Nat.* 127: 149–157.
- REINERS, W. A. 1992. Twenty years of ecosystem reorganization following experimental deforestation and regrowth suppression. *Ecol. Monogr.* 62: 503–523.
- RICHARDSON, H. L. 1938. The nitrogen cycle in grassland soils: with especial reference to the Rothamsted Park Grass Experiment. *J. Agric. Sci.* 28: 73–121.
- ROBERTS, M. R. 2004. Response of the herbaceous layer to disturbance in North American forests. *Can. J. Bot.* 82: 1273–1283.
- ROBERTS, M. R. AND H. DONG. 1993. Effects of soil organic layer removal on regeneration after clear-cutting a northern hardwood stand in New Brunswick. *Can. J. For. Res.* 23: 2093–2100.
- ROBERTS, M. R. AND F. S. GILLIAM. 2003. Response of the herbaceous layer to disturbance in eastern forests, p. 302–320. *In* F.S. Gilliam and M.R. Roberts [eds.], *The Herbaceous Layer in Forests of Eastern North America*, Oxford University Press, New York, NY.
- ROBERTS, M. R. AND L. ZHU. 2002. Early response of the herbaceous layer to harvesting in a mixed coniferous-deciduous forest in New Brunswick, Canada. *For. Ecol. Manage.* 155: 17–31.
- RUBEN, J. A., D. T. BOLGER, D. R. PEART, AND M. P. AYRES. 1999. Understory herb assemblages 25 and

- 60 years after clearcutting of a northern hardwood forest, USA. *Biol. Conserv.* 90: 203–215.
- SCHUMANN, M. E., A. S. WHITE, AND J. W. WITHAM. 2003. The effects of harvest-created gaps on plant species diversity, composition, and abundance in a Maine oak-pine forest. *For. Ecol. Manage.* 176: 543–561.
- SICCAMA, T. G., F. H. BORMANN, AND G. E. LIKENS. 1970. The Hubbard Brook ecosystem study: productivity, nutrients and phytosociology of the herbaceous layer. *Ecol. Monogr.* 40: 389–402.
- SMALL, C. J. AND B. C. MCCARTHY. 2002. The influence of spatial and temporal variability on understory diversity in an eastern deciduous forest. *Plant Ecol.* 164: 37–48.
- STIRLING, G. AND B. WILSEY. 2001. Empirical relationships between species richness, evenness, and proportional diversity. *Amer. Nat.* 158: 286–299.
- STRENGBOM, J., A. NORDIN, T. NÄSHOLM, AND L. ERICSON. 2001. Slow recovery of boreal forest ecosystem following decreased nitrogen input. *Func. Ecol.* 15: 451–457.
- STRENGBOM, J., M. WALHEIM, T. NÄSHOLM, AND L. ERICSON. 2003. Regional differences in occurrences of understory forest species reflect differences in N deposition. *Ambio* 32: 91–97.
- THOMAS, S. C., C. B. HALPERN, D. A. FALK, D. A. LIGUORI, AND K. A. AUSTIN. 1999. Plant diversity in managed forests: understory responses to thinning and fertilization. *Ecol. Appl.* 9: 864–879.
- TILMAN, D. 1987. Secondary succession and the patterns of plant dominance along experimental nitrogen gradients. *Ecol. Monogr.* 57: 189–214.
- TILMAN, D. 1989. Ecological experimentation: strengths and conceptual problems, p. 136–157. *In* G.E. Likens [ed.], *Long-Term Studies in Ecology: Approaches and Alternatives*, Springer-Verlag, New York, NY.
- ZAR, J.H. 1996. *Biostatistical analysis*, 3rd ed. Prentice-Hall, Englewood Cliffs, NJ. 662 p.