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Herbaceous layer cover and biomass in a young versus a mature stand of a central Appalachian hardwood forest[1,2]

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ABSTRACT

GILLIAM, F. S. AND N. L. TURRILL (Department of Biological Sciences, Marshall University, Huntington, WV 25755). 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. 1993.—This study examined herb layer vegetation (all vascular plants ≤1 m in height) of two montane watersheds of different stand ages in the Fernow Experimental Forest, in north-central West Virginia (WS3, ~20 yr; WS4, >80 yr). Mean herb layer cover was 19.3 and 26.4% for WS3 and WS4, respectively. Herb layer biomass was significantly ($P < 0.001$) correlated with herb cover for both watersheds. Mean herb layer biomass was 8.1 and 11.6 g/m^2 for WS3 and WS4, respectively. Herb cover responded positively to elevation on both watersheds. Within WS3, herb cover was only weakly correlated with canopy characteristics, but was positively correlated with soil pH, organic matter, sand content, cation exchange capacity, Ca, K, Mg, and NO_3-N. Within WS4, herb cover was negatively correlated with understory basal area and density, but not significantly correlated with any soil variables except Ca. From these data we suggest a hypothesis that in early forest succession in these ecosystems, early herb layer development is influenced greatly by allogenic factors (such as soil fertility) but that autogenic factors, such as canopy closure, become more important as the stand matures and becomes more stratified.

Key words: herb layer, plant-soil relationships, Central Appalachian hardwood forest.

The herbaceous layer, usually defined as all vascular plants ≤1–2 m in height (Siccama et al. 1970; Rogers 1981; Gilliam and Christensen 1986), is an important and dynamic forest stratum. Although herbaceous vegetation contributes only a small proportion of the total biomass of an ecosystem (Zavitkovski 1976), nutrient dynamics and competitive interactions within this stratum influence the initial success of plants occupying higher strata (e.g., overstory, understory, and shrub layer). In addition, productivity and nutrient relationships of herbaceous plants are often indicators of soil fertility (Chapin 1980; Peterson and Rolfe 1981; Gilliam 1988).

Herb layers of montane forests respond to a complex of environmental factors which themselves usually vary with respect to elevation. Thus, herb layer vegetation often responds to an elevational gradient in these forests (Siccama et al. 1970). These gradient factors include soil moisture (often related to soil texture), soil fertility (Siccama et al. 1970), and light availability (Anderson et al. 1969), generally a function of canopy closure. Greller (1988) stated that, within a geographical region (for example, eastern deciduous forest), herb layer cover increases with soil fertility, but that within a stand, topography and moisture are most important in influencing the herb layer. Bratton (1976) emphasized the importance of canopy structure as an integrative factor affecting the herb layer.

Few studies have focussed on herb layer response to gradient conditions and stand age. Certainly, stand age and history are known to influence herb layer cover, composition, and species diversity (Albert and Barnes 1987; Davison and Forman 1982; Brewer 1980). However, patterns of such influence can be quite site-specific. The purpose of this study was to compare cover and biomass of herb layer vegetation of a young (~20 yr) and a mature (>80 yr) watershed at a central Appalachian hardwood forest in West Virginia. Specific questions addressed were (1) what are the relationships within a watershed of herb layer vegetation to elevation and related environmental variables, such as soil factors (e.g., texture and

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nutrients) and canopy characteristics, and (2) do these relationships differ between watersheds with forests of contrasting age?

Materials and Methods. STUDY SITE. The Fernow Experimental Forest (FEF) is a 1900 ha outdoor laboratory of the Northeastern Forest Experiment Station. It is located in Tucker County, West Virginia in the Allegheny Mountain section of the unglaciated Allegheny Plateau. Precipitation averages ~145 cm/yr, mostly occurring in the growing season (Gilliam 1992). Soils of the study watersheds are mostly Alfisols derived from sandstone of the Hampshire series, typically coarse-textured (loamy sands), well-drained, and ~1 m in depth (Forest Service 1987).

The two watersheds selected for study (WS3 and WS4) are similar in most respects except stand age. WS3 and WS4 are 34.3 and 38.7 ha, respectively. WS3 (~20 yr) was clear-cut to 2.5 cm diameter breast height (dbh) in 1970 and has received aerial applications of $(NH_4)_2SO_4$ three times/yr since 1989 as part of the U.S.D.A. Forest Service Watershed Acidification Study prior to the initiation of our study. WS4 (>80 yr) was selectively cut in 1910 and has received no treatments since. Aspects for both watersheds are mostly S-SE and the range of elevation is ~740–865 m.

Both watersheds are composed of mixed hardwood stands including *Acer saccharum, Quercus rubra, Liriodendron tulipifera, Fagus grandifolia, Betula lenta,* and *Prunus serotina.* The younger WS3 has a higher number (~2400 stems/ha) of smaller stems (basal area [BA] = 24 m^2/ha). The more mature WS4 has fewer (~950 stems/ha), larger stems (BA = 38 m^2/ha) (Gilliam and Adams 1992).

SAMPLING AND DATA ANALYSIS. Fifteen circular 0.04-ha sample plots were established in each of WS3 and WS4 in locations spanning the extremes of elevation and aspect for a total of 30 sample plots for both watersheds combined. Ten circular 1-m^2 sub-plots were located within each sample plot (total number of sub-plots = 300 for both watersheds combined) by a randomized polar coordinant method to avoid oversampling the inner one-half of the plot (Gaiser 1951). All living woody stems ≥2.5 cm diameter breast height (dbh) were measured and categorized as understory (dbh ≤ 10 cm) or overstory. Within the sub-plots all vascular plants ≤1 m in height were noted for species and measured visually for cover (%) (Gilliam and Christensen 1986). For each sample plot, all above-ground material (≤1 m in height) in the two sub-plots with the greatest cover was harvested, separated by species, oven dried, and weighed (total number of harvest sub-plots = 60 for both watersheds). All sampling (tree stem measurements, herb cover estimates, herb layer harvests, and soil sampling [see below]) in both watersheds was carried out during a one-week period in mid-to-late July, 1991.

Herb cover and biomass regressions were generated from the 60 harvested sub-plots. These were used to estimate biomass for non-harvested sub-plots based on cover values of individual species within each of the other 240 sub-plots. Cover and biomass were summed for all species by sub-plot and averaged to determine mean cover (%) and biomass (g/m^2) per plot.

One 10-cm soil sample was taken from each of the two harvest subplots within each sample plot for a total of 30 soil samples per watershed. The soils were sieved to pass a 2 mm screen and air-dried. Texture was determined by the hydrometer method (Bouyoucos 1951). Texture values of subplots were averaged to yield mean sand, clay, and silt (%) per plot.

Nutrient analyses were conducted on each soil sample at the University of Maine Soil Testing Service and Analytical Lab, Orono, ME. Water pH was measured with a glass electrode. Extractable (available) Ca, K, Mg, and P were determined with plasma emission following extraction with pH 4.8 ammonium acetate (Modified Morgan extraction method). NO_3-N and NH_4-N were measured by flow-injection (colorimetric) analysis following extraction [1:10 (w:v)] with 1 N KCl. Soil organic matter was measured as percent loss on ignition by igniting subsamples at 550°C for 5 hours. Cation exchange capacity (CEC) was estimated by summation of exchangeable acidity and extractable Ca, K, and Mg. Subplot values were averaged to give mean values per plot. Plot values were averaged to give mean values per watershed.

Significant differences between watershed means were compared using *t*-tests. Relationships of herb layer cover to soil and canopy to soil and canopy variables (basal area and density) were assessed using Pearson product-moment correlations based on individual plot values (Zar 1973).

Results. Regression of herb biomass to cover produced the following equation,

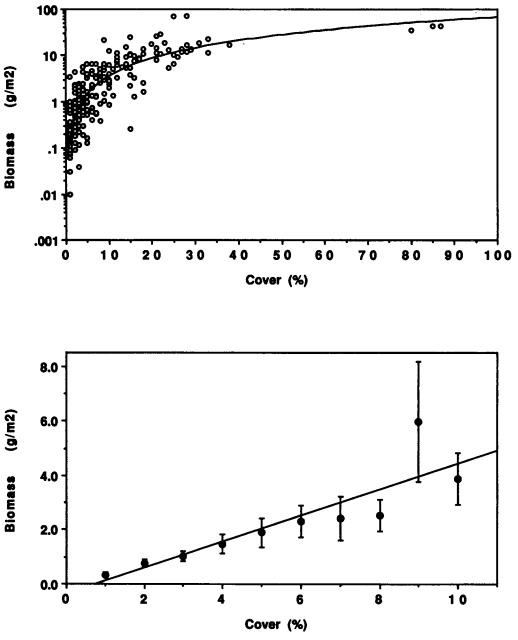

Fig. 1. Relationship of biomass to cover of individual herb species within 1-m² plots. a) All individual species combined. Equation for line is $y = 0.18x^{1.29}$, $r^2 = 0.71$, $P < 0.001$. b) All individuals ≤10% cover. Values are mean biomass (±1 SE) for each cover value. Equation for line is $y = -0.38 + 0.48x$, $r^2 = 0.77$, $P < 0.001$.

$$y = 0.18x^{1.29} \quad (1)$$

where y is biomass (g/m²), x is cover (%); $r^2 = 0.71$, $P < 0.001$ (Fig. 1a). It should be noted that each data point in Fig. 1a represents individual species values per subplot from both WS3 and WS4. Regressions of each watershed separately were not significantly different; thus, the curve shown is a regression for all data combined. Due to the abundance of low cover individuals within both harvest and non-harvest sub-plots, these relationships were further analyzed by examining mean herb biomass within each of 1–10% cover classes. This regression produced the following equation,

$$y = -0.38 + 0.48x \quad (2)$$

where y is biomass (g/m²), x is cover (%); $r^2 = 0.77$, $P < 0.001$ (Fig. 1b). Equation (1) was used to estimate biomass for individual species which had cover of >10%; equation (2) was used for species with cover ≤10%.

Table 1. Herb layer characteristics of Watersheds 3 and 4 of the Fernow Experimental Forest, Parsons, WV. Values given are means ± 1 SE. Species diversity calculated with the Shannon-Wiener Index using natural log transformations of cover values.

Characteristic	Watershed	
	WS3	WS4
Cover (%)	19.3 ± 3.7	26.4 ± 4.3
Biomass (g/m²)	8.1 ± 2.2	11.6 ± 2.6
Species richness (#/m²)	3.6 ± 0.2	3.7 ± 0.5
Species diversity (H′)	1.71 ± 0.11	1.85 ± 0.10

Table 2. Correlation matrices for herb layer and stand characteristics of two watersheds of Fernow Experimental Forest, Parsons, WV. Pearson product-moment correlation coefficients are given only if significant at $P < 0.05$. Characteristics are herb cover (HCOV), elevation (ELEV), overstory density (ODENS), understory density (UDENS), overstory basal area (OBA), and understory basal area (UBA).

	HCOV	ELEV	ODENS	UDENS	OBA
WS3					
ELEV	0.74*				
ODENS	—	—			
UDENS	—	—	—		
OBA	0.55	0.53	0.74*	—	
UBA	−0.54	—	—	0.79*	0.47
WS4					
ELEV	0.54				
ODENS	—	—			
UDENS	−0.73*	−0.68*	—		
OBA	—	—	—	—	
UBA	−0.69*	−0.55	—	0.73*	—

* $P < 0.01$.

Herb layer cover and biomass showed no significant differences between watersheds (Table 1) and increased with increasing elevation on both WS3 and WS4 (Table 2). Because of the close relationship of herb layer biomass to herb layer cover, and that biomass was calculated from a model based on cover, further discussion of herb layer vegetation will mention only cover, with direct implications for biomass. WS3 and WS4 were also very similar in terms of important herb layer species, based on mean cover per watershed (Table 3).

There were virtually no significant differences between watersheds for any soil variables. The soils of WS3 and WS4 were strongly acidic, with moderate CEC and base saturation (~25%) (Table 4). Available P was slightly but significantly ($P < 0.05$) higher in WS4. NO_3 was the dominant form of available N on both watersheds (Table 4).

On WS3, herb cover was positively correlated

Table 3. Important species (ranked by cover) of WS3 and WS4 of the Fernow Experimental Forest, Parsons, WV. Values given are mean cover per watershed. Nomenclature follows Strausbaugh and Core (1977).

Species	Watershed WS3 Cover (%)	WS3 Rank	WS4 Cover (%)	WS4 Rank
Laportea canadensis	4.6	1	7.7	1
Viola spp.	3.1	2	2.2	3
Smilax rotundifolia	2.8	3	1.4	6
Acer pensylvanicum	1.4	4	2.5	2
Rubus spp.	1.3	5	1.1	8
Lycopodium flabelliformes	1.2	6	—	
Sassafras albidum	0.9	7	—	
Dryopteris spinulosa	0.5	8	1.1	9
Prunus serotina	0.5	9	0.9	10
Sedum ternatum	0.3	10	—	
Polystichum acrostichoides	0.2	11	1.7	4
Polygonatum biflorum	0.2	12	0.8	11
Vaccinium vacillans	—		1.4	5
Acer saccharum	—		1.1	7
Caulophyllum thalictroides	—		0.6	12

($P < 0.05$) with overstory basal area and negatively correlated ($P < 0.05$) with understory basal area (Table 2). However, herb cover was more highly (positively) correlated with several soil variables, including soil texture ($P < 0.01$), organic matter and NO_3-N ($P < 0.001$), and pH, CEC, Ca, K, and Mg ($P < 0.0001$) (Table 5). In sharp contrast, herb cover on WS4 was negatively correlated ($P < 0.01$) with understory basal area and density (Table 2) and, except for Ca, was not related to any soil variables (Table 5).

Discussion. For watersheds with greatly differing stand ages, WS3 and WS4 were remarkably similar in many soil and herb layer characteristics. Similarities in soil chemistry and physical structure (Table 4) suggest that there is little or no inherent variation between watersheds based on parent material differences. These results were similar to those of Albert and Barnes (1987) who found that soil texture and soil pH, Ca, and Mg were not significantly different between previously cut (~50 yr) and uncut (age not given) areas of a Michigan deciduous forest.

Despite differences in stand age, WS3 and WS4 were quite comparable in herb layer diversity (H′) and species richness, defined here as the mean number of species/m^2 sub-plot (Table 1). Our richness values were less than the 5.5 species/m^2 of a 55-yr old watershed at Hubbard Brook Experimental Forest (Siccama et al. 1970).

Similarities between watersheds were also seen

Table 4. Mean physical and chemical characteristics of soils from two watersheds of the Fernow Experimental Forest, Parsons, WV. Values given are mean ± 1 SE.

Soil variable	Watershed WS3	WS4
pH	4.3 ± 0.1	4.2 ± 0.1
CEC (meq/100 g)	5.1 ± 0.9	4.1 ± 0.1
Organic matter (%)	14.2 ± 1.2	13.8 ± 0.5
Sand (%)	65.7 ± 1.9	66.0 ± 1.5
Clay (%)	12.0 ± 0.9	10.7 ± 0.7
Silt (%)	22.2 ± 1.4	23.3 ± 1.2
Macronutrients (μeq/g)		
Ca	15.6 ± 9.4	4.7 ± 0.4
K	2.3 ± 0.3	2.1 ± 0.1
Mg	2.5 ± 0.8	1.6 ± 0.1
P	1.2 ± 0.1*	1.4 ± 0.1
NO_3-N	2.4 ± 0.4	1.9 ± 0.3
NH_4-N	0.9 ± 0.1	0.7 ± 0.1

* Significant difference between watersheds at $P < 0.05$.

in species composition. Most of the important herb layer species were found in both watersheds (Table 3). These included wood nettle (*Laportea canadensis* (L.) Wedd.), violets (*Viola* spp.), greenbrier (*Smilax rotundifolia* L.), striped maple seedlings (*Acer pensylvanicum* L.), and raspberry (*Rubus* spp.). The main difference between young and mature stands was an increase in older stands in cover of shield fern (*Dryopteris spinulosa* (O.F. Muell.) Watt.) and Christmas fern (*Polystichum acrostichoides* (Michx.) Schott) (Table 3), both of which are considered shade-

Table 5. Pearson product-moment correlation coefficients of herb cover and soil variables for two watersheds of the Fernow Experimental Forest, Parsons, WV. Values given are significant to $P < 0.01$.

Soil variable	Watershed WS3	WS4
pH	0.90**	—
CEC (meq/100 g)	0.84**	—
Organic matter (%)	0.81*	—
Sand (%)	0.73	—
Clay (%)	−0.69	—
Silt (%)	—	—
Macronutrients (meq/100 g)		
Ca	0.86**	0.66
K	0.87**	—
Mg	0.88**	—
P	—	—
NO_3-N	0.80*	—
NH_4-N	—	—

* $P < 0.001$.
** $P < 0.0001$.

Table 6. Herbaceous layer cover and biomass from selected eastern deciduous forests.

Site (source)	Forest type	Cover (%)	Biomass (g/m^2)
Appalachian hardwood forest, WV (present study)	WS3	19.3	13.0
	WS4	26.4	11.6
Northern hardwood forest, NH (Siccama et al. 1970)	maple-beech	24.0	7.0
Appalachian oak forest, VA (McEvoy et al. 1980)	oak-hickory	9.6	11.0
Appalachian old-growth forest, WV (Maguire 1979)	hemlock-hardwood	36.8	—
Northern hardwood forest, NJ (Davison and Forman 1982)	oak-hickory	31.0	—
Northern hardwood forest, IL (Bazzaz and Bliss 1970)	oak-hickory	—	68.0
Northern hardwood forest, IL (Peterson and Rolfe 1982)	oak-hickory (upland)	—	24.5
	silver maple (floodplain)	—	88.8
Northern hardwood forest, WI (Zavitkovski 1976)	aspen	—	117.5
	maple-aspen-birch	—	63.0
	birch	—	51.0

tolerant or "shade-obligate" (sensu Greller 1988). Again, these results support those of Albert and Barnes (1987), who found few differences in herb layer composition between cut and uncut deciduous forests in Michigan.

Herb layer biomass of WS3 and WS4 were on the low end of the 10–100 g/m^2 range reported by Ovington (1962) for temperate forest herbs. Our biomass values were similar to those of the Hubbard Brook Experimental Forest (Siccama et al. 1970), but decidedly lower than values reported for other eastern deciduous forests in the literature (Table 6). Our herb cover data were comparable to those of other studies (Table 6).

Because of the differences in stand age of these adjacent watersheds, our data have implications for successional change in herb layer development in hardwood forests. Following clear-cutting in hardwood forests, ground ("herb layer") cover generally increases rapidly as a mixture of sprouts of woody and perennial herbaceous species, as well as seedlings from buried seeds. Bormann and Likens (1979) viewed this as a single undifferentiated stratum (i.e., not true herb layer). On another watershed at FEF (WS7, adjacent to WS3), Kochenderfer and Wendel (1983) showed that ground cover and stratum differentiation increased rapidly in the first 10 yr following release from clear-cut/herbicide treatment. In an oak forest, Davison and Forman (1982) showed increase in herb layer cover over a 20-yr period, with little cover change thereafter. Thus, herb cover similarities between our young (~20 yr) WS3 and mature (>80 yr) WS4 may indicate that herb cover varies temporally very little in these forests after ~20 yr, similar to results of Davison and Forman (1982).

Although overall (mean) herb layer cover was very similar for WS3 and WS4 and cover increased significantly with elevation within both watersheds (Table 2), specific factors affecting herb cover appeared to vary greatly between watersheds, suggesting stand age-related change in herb layer response. Whereas herb layer cover appeared to respond positively to soil fertility on WS3, herb cover on WS4 showed no response to fertility (Table 5). Similarly, herb cover was highly negatively correlated with understory density and basal area on WS4, whereas herb cover on WS3 showed less highly significant correlations with overstory and understory basal area (Table 2).

Even though stand differentiation begins quickly following cutting, full differentiation (stratification) into overstory and understory strata probably does not occur in these forests until >60 yr (Bormann and Likens 1979). Indeed, data from Gilliam and Adams (1992) indicate that WS3 is a relatively unstratified, even-aged stand, whereas WS4 is mixed-aged with distinct overstory and understory strata. Thus, our data suggest that herb layer development on WS4 may be responding to change in light availability created by variation in the understory (Table 2).

Greller (1988) cites moisture ("soil drainage") as an important factor influencing herb layer development within hardwood stands. We did not determine water availability indices for our soils, but water availability is usually closely related to the clay content of the soil (Jenny 1980). Thus, if water availability is a determinant factor within a stand, one would expect a positive relationship between herb cover and clay content (%) of the soil. Herb cover was negatively correlated with clay content on WS3 and not correlated with clay content on WS4 (Table 5). Thus, although

we did not measure soil moisture in this study, we feel that water availability may not be a major factor determining herb layer patterns in these watersheds. This is not surprising considering that precipitation at FEF averages >140 cm/yr, most of which occurs during the growing season (Gilliam 1992).

In conclusion, results of our study suggest that 1) the herb layer responds to soil factors and stand structure, both of which can vary greatly with elevation in montane hardwood forests, but that 2) the patterns of these herb layer responses may change through successional time. It is a reasonable hypothesis from these data that, for this forest type, early in succession, when light availability is relatively uniform and high in a watershed, herb layer development is nutrient limited. Later in succession, canopy stratification and closure increase and the herb layer becomes more limited by light availability.

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