

Composition and Structure of Two Old-growth Forest Ecosystem Types of Southeastern Ohio¹

P. CHARLES GOEBEL, DAVID M. HIX, AND MARIE SEMKO-DUNCAN, School of Natural Resources, Ohio Agricultural Research and Development Center, The Ohio State University, 1680 Madison Ave, Wooster, OH 44691; School of Natural Resources, The Ohio State University, 2021 Coffey Road, Columbus, OH 43210-1085

ABSTRACT. Less than 1% of the pre-European settlement forest in Ohio currently remains, mostly as small and scattered woodlots. Consequently, few studies have been undertaken to quantify the composition and structure of Ohio's old-growth forests using a landscape ecosystem perspective. We used an existing multifactor ecosystem classification system developed for the Wayne National Forest in southeastern Ohio to compare the composition and structure of two old-growth forest ecosystem types, located on contrasting north-facing and south-facing middle slopes. No differences in physiography were observed among the stands other than aspect; however, the north-facing old-growth ecosystem type had a greater A horizon thickness and a higher pH than the south-facing old-growth ecosystem type. Mixed-oaks dominate the south-facing ecosystem type, while sugar maple, American beech and northern red oak dominate the north-facing ecosystem type. No differences were detected in stand structural components. Similar trends were observed for the ground-flora layer; specifically, we observed differences in ground-flora composition between the two ecosystem types but no differences in total percent cover or species richness. Finally, the composition and structure of coarse woody debris differed between the contrasting ecosystem types. Maple and oak snags and fallen logs dominate the north-facing ecosystem while oak standing snags and fallen stems are typically observed in the south-facing ecosystem. Few differences between the two ecosystem types were detected in coarse woody debris structure, except that snag density tends to be higher in the south-facing old-growth ecosystem and log density and volume tends to be higher in the north-facing ecosystem ($P < 0.10$). Through the use of this ecosystem approach, we can begin to quantify the ecological factors regulating the composition and structure of old-growth communities, improving our ability to effectively manage and restore these rare ecosystems.

OHIO J SCI 105 (2):8-16, 2005

INTRODUCTION

Although humans and forest ecosystems often interact in complex and synergistic ways, individual old-growth stands or forests typically represent an undisturbed condition where the influence of geomorphology, soils, and natural disturbances, in conjunction with plant reproductive processes and animals, constrain the development of plant communities (Rowe and Sheard 1981; Pregitzer and others 2001). Old-growth forests are generally considered to represent the final, stable phase of stand development and typically are recognized by the unique structural characteristics they share. For example, eastern old-growth forests are usually described as multi-aged stands with multiple structural layers, large amounts of coarse woody debris (both dead snags and fallen logs), undisturbed soils, and a diverse array of both plants and animals (Parker 1989; Leverett 1996). Ecosystem processes, including nutrient cycling, stability, and biodiversity, are also believed to remain undisturbed in old-growth forests (Leverett 1996; Meier and others 1996).

In Ohio, as well as across the Central Hardwoods Region, the remaining isolated old-growth tracts have been the focus of old-growth preservation and recovery programs (Trombulak 1996). These remnant and isolated woodlots may be seen as analogous to museum

archives, revealing little about the overall landscape or interactions among forest ecosystems at the time of European settlement. Additionally, many of these remnant old-growth stands are in transition. Land-use practices in the surrounding landscape, such as fire suppression, are resulting in compositional and structural changes in these old-growth forests (Goebel and Hix 1996, 1997). Because the composition and structure of individual old-growth stands is influenced strongly by the dispersal patterns of individual species, site history, and environmental factors, the focus of old-growth preservation must occur at the ecosystem level and focus on preserving the 'natural' processes of old-growth forests (Barnes 1989; Pickett and Parker 1994; Trombulak 1996).

Ecosystem classification is a useful tool that facilitates the understanding of interrelationships among plant communities and the environment and how these factors influence ecosystem restoration decisions (Palik and others 2000). Ecosystem classifications define ecosystems hierarchically, as volumes of earth, air, and water with specific developmental histories in which plants and animals live and interact (Rowe and Barnes 1994; Barnes and others 1998). In Ohio, there has been some research published concerning the composition and structure of particular old-growth tracts (for example, McCarthy and others 1987; Cho and Boerner 1991; McCarthy and others 2001). However, very little is known about the compositional and structural variation among Ohio's old-growth forest ecosystems in relation to the hierarchical

¹Manuscript received 19 May 2003 and in revised form 2 October 2003 (#03-11).

factors regulating their composition and structure, especially physiography and soils. By applying the ecosystem classifications developed for the Wayne National Forest (Hix and Percy 1997; Hix and others 1997), old-growth conditions of individual forest ecosystems of southeastern Ohio can be described and compared, ultimately leading to improved programs to manage and restore these threatened ecosystems.

Using the ecosystem classification developed for the Athens Unit of the Wayne National Forest as a framework, in this paper we: 1) examine the physiographic and edaphic factors that regulate overstory and ground-flora vegetation of two old-growth forest ecosystems in southeastern Ohio; and 2) examine the physiographic constraints on coarse woody debris (CWD) composition and structure between the two old-growth forest ecosystems.

MATERIALS AND METHODS

Study Area

The study area is located in the Western Hocking Plateau Subsection (221Ef) of the Southern Unglaciated Allegheny Plateau Section (221E) in the Eastern Broadleaf Forest Province (Keys and others 1995). The Subsection is described as a maturely dissected plateau with moderate to steep slopes, narrow ridgetops, rock outcrops, and narrow stream valleys with elevations ranging from 195 to 322 m above sea level. Geology of the study area consists of inter-bedded sedimentary bedrock of shale, siltstone, limestone, and coal that was laid down in the shallow seas of the Mississippian, Pennsylvanian, or Permian periods in an anticline that dips eastward to the Appalachian Geosyncline (Rypma 1961; Keys and others 1995). In general, the soils are moderately acidic with surface layers that are moderately drained to well-drained loams or silt loams, and with subsoils comprised of silty clays, loamy clays, or clays.

The climate of the area is humid continental with a mean annual temperature of 9° C (Lucht and others 1985). Winters are relatively cold, while summers are generally warm with a mean July maximum temperature of 32.2° C and a mean January minimum temperature of 6.9° C (Athens weather station; Lucht and others 1985). Average annual precipitation is 98 cm, half of which falls from May to October (Lucht and others 1985). The topographic variability associated with the study area is responsible for significant differences in microclimate, which are common. A ridge system oriented from northwest to southeast occurs over most of the study area. This results in southerly-facing slopes that receive higher levels of solar radiation and, consequently, have higher air and soil temperatures, lower relative humidity, and lower soil moisture than their northerly-facing counterparts.

Field Methods

Eight old-growth stands (defined as stands >150 year old; see Goebel and Hix 1996; Olivero and Hix 1998 for information on how these stands were identified) were selected within two contrasting ecosystems using a multi-factor ecological classification system (ECS) based on climate, physiography, soils, and vegetation developed

recently for the Athens Unit of the Wayne National Forest in southeastern Ohio (Table 1). These included: 1) north-facing mesic slopes (ELTP 42 – mesic middle slopes), and 2) south-facing dry slopes (ELTP 32 – dry upper to middle slopes). Two sample plots were then established randomly on a transect that roughly bisected the stand along the contour. The first plot was located randomly 20 to 30 m from the boundary, and the second plot was installed randomly at least 40 to 50 m from the first plot. Each sample plot consisted of a circular 500-m² plot and eight rectangular 1.0 m × 2.0 m quadrats. The centers of the quadrats were located 7.0 m from the center of the 500-m² plots in eight directions (N, NE, E, SE, S, SW, W, NW).

At the center of each plot the following physiographic features were observed or measured: aspect (azimuth in degrees), slope steepness (%), slope shape (concave, linear, or convex), length of slope, distance to nearest surface water, and the distance to the ridgetop. The percentage of the distance to the ridgetop (PDR) was calculated by dividing the distance to the ridgetop by the total length of the slope. The elevation of each plot was determined from a topographic map. Surface soil characteristics were also measured on each plot. Thickness and texture (determined by feel in the field) of the A horizon was estimated by averaging eight push-tube samples randomly located across the plot. Push-tube samples for each plot were placed in sample bags and pH of the A horizon determined in the lab using the calcium chloride method (McLean 1982).

On each 500-m² plot, the species, dbh (diameter at breast height; 1.37 m), and crown class (dominant, co-dominant, intermediate, and overtopped; compare Smith 1986) of all living overstory trees >10.0 cm dbh was recorded. Dead snags >10.0 cm dbh were also tallied by species and dbh on each 500-m² plot. Heights of the snags to the nearest meter were recorded using a clinometer. Data on the fallen trees >10.0 cm mid-diameter included species and length. Although not all snags and fallen trees were determinable to species, it was possible to determine the genus of each snag and fallen tree. Ground-flora vegetation (vascular plants <1 m tall, including pteridophytes, graminoids, forbs, woody vines, and shrubs) was sampled in each of the eight 1.0 × 2.0 m quadrats on each plot. Percent coverage was estimated visually for each ground-flora species in a quadrat using the following cover class codes: 1, <1%; 2, 1-5%; 3, 6-10%; 4, 11-20%; 5, 21-40%; 6, 41-70%; 7, 71-100%.

Data Analyses

Importance values (IV) were calculated for overstory trees as the summation of relative density and relative dominance (as expressed by basal area) divided by 2. Mean cover for each ground-flora species by plot was calculated by averaging cover class values from the eight quadrats. Mean diameter, height (m), density (stems/ha), basal area (m²/ha) and volume (m³/ha) of each standing dead species (snags) were computed for each plot. Similarly, the average mid-diameter, density, and volume of fallen dead stems (CWD) were also calculated.

Canonical correspondence analysis (CCA) was used to

TABLE 1

Classification of ecological landtypes (ELTs) and ecological landtype phases (ELTPs), Athens Unit, Wayne National Forest, southeastern Ohio (Goebel and Hix 1997). Old-growth ecosystems compared in this study are highlighted.

I. Level to gently sloping terrain (0-15%)	
ELT 1	Broad Level Uplands
ELT 2	Narrow Uplands
ELTP 20	Dry ridgetops; white oak-black oak/blueberry
ELT 5	Narrow Bottomlands
ELTP 50	Wet-mesic ravine bottoms; American basswood-yellow buckeye/jack-in-the-pulpit
ELT 6	Broad Bottomlands
II. Moderately to very steeply sloping terrain (>15%)	
ELT 3	Dry Slopes with southerly aspects (136-315°)
ELTP 31	Dry upper slopes; white oak/tick-trefoil
ELTP 32	Dry upper to middle slopes; white oak-chestnut oak/greenbrier
ELTP 33	Dry-mesic lower slopes; red maple-white oak/goldenrod
ELT 4	Mesic Slopes with northerly aspects (316-135°)
ELTP 41	Dry-mesic upper slopes; Northern red oak-white oak/enchanter's nightshade
ELTP 42	Mesic middle slopes; yellow buckeye-American beech/maidenhair fern
ELTP 43	Mesic middle to lower slopes; white ash-northern red oak/geranium
ELTP 44	Mesic lower slopes; sugar maple/cleavers

explore the variation in species composition and site factors between the two types of old-growth ecosystem types (CANOCO; ter Braak and Smilauer 1998). Canonical correspondence analysis is an eigenvector ordination technique that provides a multivariate direct gradient analysis that helps to visualize patterns of community variation and the influence of environmental factors on species distributions (ter Braak and Smilauer 1998). CCA was performed separately on both the overstory and ground-flora datasets.

Differences in site factors and stand structure between the two types of old-growth ecosystems were measured using a Mann-Whitney test ($P = 0.05$). The Mann-Whitney test is a non-parametric test for two samples that does not require assumptions of normality or equal variance (Kent and Coker 1992). Mann-Whitney tests were conducted for both the overstory and ground-flora vegetation layers, as well as for the coarse woody debris.

RESULTS

Site Factors

No differences in slope percent or PDR are detected between the two old-growth ecosystems, suggesting that both are located on steeply sloping middle slopes. However, we did detect significant differences in aspect between the two old-growth ecosystems. These results

confirm the classification of the individual stands into either ELTP 32 or ELTP 42 as prescribed by the Wayne National Forest ecosystem classification (Table 1). Corresponding to the different topographic positions, Mann-Whitney tests reveal that A horizon thickness and pH are significantly higher for the north-facing old-growth ecosystem compared to the south-facing old-growth ecosystem ($P < 0.05$; Table 2).

TABLE 2

Site factors for north-facing and south-facing old-growth ecosystems in southeastern Ohio. Values are means ± 1 standard error. Values in a row followed by the same letter are not significantly different at $P < 0.05$ (Mann-Whitney test).

Variable	North-Facing	South-Facing
Transformed Aspect	1.72 (0.09) <i>a</i>	0.16 (0.05) <i>b</i>
Percent Slope (%)	27.4 (2.6) <i>a</i>	28.9 (2.3) <i>a</i>
Percent distance to ridgetop (PDR)	45.6 (6.0) <i>a</i>	52.3 (3.0) <i>a</i>
Thickness of A horizon (cm)	7.0 (0.9) <i>a</i>	3.5 (0.6) <i>b</i>
pH of A horizon	5.0 (0.3) <i>a</i>	3.3 (0.1) <i>b</i>

Overstory

Mixed-oaks (*Quercus* spp.) dominate the south-facing stands, while sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and northern red oak (*Quercus rubra* L.) dominate the north-facing stands (Table 3). Overstory composition accounts for 45% of the variation among old-growth ecosystems along the first two canonical axes, separating the north-facing and south-facing old-growth ecosystems along the first axis of the overstory CCA (Fig. 1). First and second axis overstory and stand-site factor correlation coefficients are very high (0.99 and 0.97, respectively); both axes combine to explain over half (55.4%) of total variation among old-growth ecosystems as explained by the site factors included in the CCA. While slope shape, PDR, and slope percent explains little of the variation among old-growth ecosystems, aspect and corresponding soil characteristics (A horizon thickness and A horizon pH) are strongly associated with the first canonical axis (Fig. 1).

Although overstory composition is different between the two old-growth ecosystems, no significant differences in stand structure are detected ($P > 0.05$; Table 3). Basal area in the north-facing old-growth ecosystem averages (± 1 SE) 30.4 (4.2) m^2/ha , while density averages 362 (22) stems/ha. Values of basal area and density are similar for the south-facing old-growth ecosystem, averaging 30.8 (2.7) m^2/ha and 332 (25) stems/ha, respectively. Similarly, no differences in richness are detected ($P > 0.05$) between the north-facing and south-facing stands (Table 3).

TABLE 3

Overstory importance values[†], richness, basal area, and density for north-facing and south-facing old-growth ecosystems in southeastern Ohio. Values are means \pm 1 standard error. Values in a row followed by the same letter are not significantly different at $P < 0.05$ (Mann-Whitney test).

Species Name	Code	Importance Value [†]	
		North-Facing	South-Facing
<i>Acer rubrum</i>	ACRU	6.4 (4.3) <i>a</i>	8.8 (2.3) <i>a</i>
<i>Acer saccharum</i>	ACSA3	42.1 (8.5) <i>a</i>	7.5 (2.6) <i>a</i>
<i>Aesculus flava</i>	AEFL	9.2 (3.9)	–
<i>Carya cordiformis</i>	CACO15	–	0.5 (0.5)
<i>Carya glabra</i>	CAGL18	3.4 (1.9) <i>a</i>	0.5 (0.5) <i>a</i>
<i>Carya ovata</i>	CAOV2	–	0.5 (0.5)
<i>Carya alba</i>	CAAL	1.1 (1.1)	–
<i>Fagus grandifolia</i>	FAGR	8.4 (3.9) <i>a</i>	3.1 (1.6) <i>a</i>
<i>Liriodendron tulipifera</i>	LITU	3.2 (3.2) <i>a</i>	1.3 (1.3) <i>a</i>
<i>Nyssa sylvatica</i>	NYSY	0.9 (0.9) <i>a</i>	1.0 (1.0) <i>a</i>
<i>Oxydendron arboreum</i>	OXAR	–	0.5 (0.5)
<i>Prunus serotina</i>	PRSE2	2.4 (1.9) <i>a</i>	0.4 (0.4) <i>a</i>
<i>Quercus alba</i>	QUAL	5.4 (3.6) <i>a</i>	35.7 (7.9) <i>b</i>
<i>Quercus coccinea</i>	QUCO2	1.8 (1.8) <i>a</i>	1.3 (0.9) <i>a</i>
<i>Quercus prinus</i>	QUPR2	2.3 (2.3) <i>a</i>	23.4 (8.5) <i>b</i>
<i>Quercus rubra</i>	QURU	10.6 (5.3) <i>a</i>	4.8 (2.0) <i>a</i>
<i>Quercus velutina</i>	QUVE	–	9.4 (2.1)
<i>Sassafras albidum</i>	SAAL5	0.4 (0.4) <i>a</i>	0.8 (0.5) <i>a</i>
<i>Ulmus rubra</i>	ULRU	1.7 (1.2)	–
Structural Characteristics			
Richness (no. of species)		15 <i>a</i>	16 <i>a</i>
Basal area (M ² ha ⁻¹)		30.4 (4.2) <i>a</i>	30.8 (2.7) <i>a</i>
Density (stems ha ⁻¹)		362 (22) <i>a</i>	332 (25) <i>a</i>

Importance value = (relative dominance + relative density)/2.

Ground-flora

The characteristic ground-flora species of the north-facing old-growth ecosystem include *Actaea pachypoda* Ell., *Circaea lutetiana* L., *Osmorhiza claytoni* (Michx.) C.B. Clarke, *Viola pubescens* Ait., and *Polygonum virginianum* L., while the ground-flora of the south-facing old-growth ecosystem are dominated by *Smilax rotundifolia* L., *Solidago caesia* L., *Carex blanda* Dewey, and *Desmodium nudiflorum* (L.) DC. (Table 4). The CCA relating site factors to the ground-flora composition accounts for 33.1% of the variation among old growth stands; site factors combine to explain over 55.0% of the total variation in ground-flora composition along the first two axes. Similar to the overstory CCA, aspect and corresponding A horizon soil characteristics are strongly associated with the first canonical axis, separating the

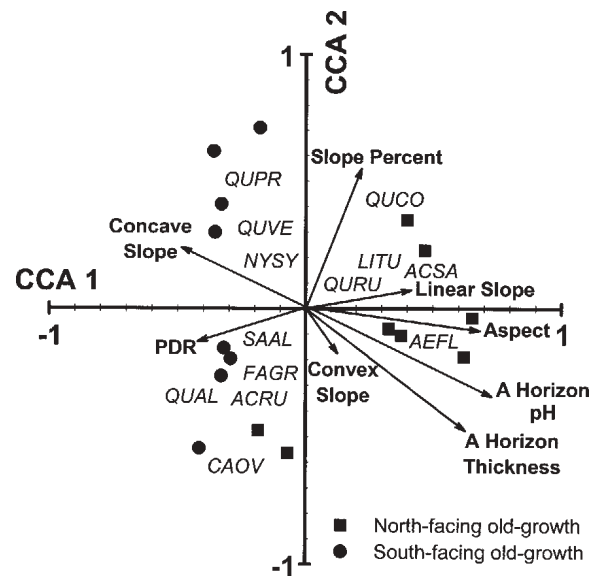


FIGURE 1. Overstory canonical correspondence analysis (CCA) triplot of old-growth ecosystems in southeastern Ohio. (See Table 3 for species acronym codes.)

north-facing and south-facing ecosystems (Fig. 2).

Mean ground-flora percent cover is not significantly different between old-growth ecosystems ($P > 0.05$). Likewise, ground species richness was not significantly different between the south-facing old-growth ecosystem and the north-facing old-growth ecosystem ($P > 0.05$; Table 4).

Coarse Woody Debris

Both dead snags and fallen trees differ in composition between the two old-growth ecosystems. *Acer* and *Quercus* snags dominate the north-facing ecosystem (relative densities of 56% and 28%, respectively), while only *Quercus* snags are typically observed in the south-facing ecosystem (relative density of 68%) (Table 5). Likewise, the north-facing ecosystems have high proportions of *Quercus* and *Acer* fallen trees (relative densities of 31% and 11%, respectively), while the south-facing old-growth ecosystem is comprised predominantly of *Quercus* CWD (relative density of 84%) (Table 5). Over half (57%) of the fallen trees in the north-facing old-growth ecosystem are highly decayed and unidentifiable compared to only 7% in the south-facing ecosystem type.

Fewer, larger snags are found in the north-facing old-growth ecosystem than in the south-facing ecosystem, although these differences are not significant ($P > 0.05$; Fig. 3). On average (\pm 1 SE) the diameter at breast height of snags in the north-facing old-growth ecosystem is 32.5 (10.0) cm, while only 24.3 (4.4) cm in the south-facing old-growth ecosystem. Snag density averages 27.5 (8.4) stems/ha in the north-facing stands and 45.0 (9.0) stems/ha in the south-facing stands. Total snag volume tends to be higher in the north-facing ecosystem than the south-facing ecosystem; however, total snag volume was extremely variable (Fig. 3).

As with snag structure, the structure of fallen trees is

TABLE 4

Ground-flora mean cover values and richness for north-facing and south-facing old-growth ecosystems in southeastern Ohio. Values are means \pm 1 SE. Values in a row followed by the same letter are not significantly different at $P < 0.05$ (Mann-Whitney test).

Species Name	Code	Mean Cover	
		North-Facing	South-Facing
<i>Actaea pachypoda</i>	ACPA	0.23 (0.10)	–
<i>Adiantum pedatum</i>	ADPE	0.05 (0.05)	–
<i>Amphicarpa bracteata</i>	AMBR2	–	0.02 (0.02)
<i>Antennaria plantaginifolia</i>	ANPL	–	0.05 (0.03)
<i>Thalictrum thalictroides</i>	THTH2	0.05 (0.05) <i>a</i>	0.10 (0.07) <i>a</i>
<i>Aristolochia serpentaria</i>	ARSE3	0.02 (0.02)	–
<i>Arisaema triphyllum</i>	ARTR	0.02 (0.02) <i>a</i>	0.05 (0.03) <i>a</i>
<i>Asarum canadense</i>	ASCA	–	0.30 (0.14)
<i>Eurybia divaricata</i>	EUDI16	0.14 (0.09) <i>a</i>	0.53 (0.18) <i>a</i>
<i>Eurybia macrophylla</i>	EUMA27	0.05 (0.03)	–
<i>Asimina triloba</i>	ASTR	0.22 (0.22) <i>a</i>	0.13 (0.10) <i>a</i>
<i>Botrychium virginianum</i>	BOVI	0.09 (0.06)	–
<i>Carex albursina</i>	CAAL11	0.06 (0.05)	–
<i>Carex blanda</i>	CABL	0.03 (0.03) <i>a</i>	0.13 (0.07) <i>a</i>
<i>Carex digitalis</i>	CADI5	–	0.02 (0.02)
<i>Carex gracilescens</i>	CAGR8	0.08 (0.06)	–
<i>Carex rosea</i>	CARO22	0.08 (0.04)	–
<i>Celastrus scandens</i>	CESC	0.08 (0.05) <i>a</i>	0.02 (0.02) <i>a</i>
<i>Chimaphila maculata</i>	CHMA3	–	0.20 (0.16)
<i>Circaea lutetiana</i>	CILU	0.28 (0.11) <i>a</i>	0.05 (0.03) <i>b</i>
<i>Cimicifuga racemosa</i>	CIRA	0.06 (0.06)	–
<i>Collinsonia canadensis</i>	COCA4	0.02 (0.02) <i>a</i>	0.03 (0.03) <i>a</i>
<i>Cunila origanoides</i>	CUOR	–	0.05 (0.03)
<i>Danthonia spicata</i>	DASP2	–	0.03 (0.02)
<i>Desmodium nudiflorum</i>	DENU4	–	0.42 (0.23)
<i>Disporum lanuginosum</i>	DILA5	0.27 (0.17)	–
<i>Eupatorium purpureum</i> var. <i>purpureum</i>	EUPUP	–	0.14 (0.07)
<i>Ageratina altissima</i> var. <i>altissima</i>	AGALA	0.09 (0.04) <i>a</i>	0.06 (0.03) <i>a</i>
<i>Festuca subverticillata</i>	FESU3	0.13 (0.13)	–
<i>Galium circaezans</i>	GACI2	0.11 (0.06) <i>a</i>	0.03 (0.03) <i>a</i>
<i>Galium concinnum</i>	GACO3	0.30 (0.15) <i>a</i>	0.08 (0.04) <i>a</i>
<i>Galium lanceolatum</i>	GALA3	0.03 (0.03) <i>a</i>	0.03 (0.02) <i>a</i>
<i>Galium triflorum</i>	GATR3	0.03 (0.03) <i>a</i>	0.03 (0.02) <i>a</i>
<i>Geum canadense</i>	GECA7	0.08 (0.08)	–
<i>Geranium maculatum</i>	GEMA	0.28 (0.12) <i>a</i>	0.06 (0.03) <i>a</i>
<i>Goodyera pubescens</i>	GOPU	0.03 (0.03) <i>a</i>	0.03 (0.02) <i>a</i>
<i>Hepatica nobilis</i> var. <i>obtusa</i>	HENOO	0.03(0.02)	–
<i>Hydrastis canadensis</i>	HYCA	0.05 (0.05)	–
<i>Lindera benzoin</i>	LIBE3	1.02 (0.58) <i>a</i>	0.17 (0.09) <i>a</i>
<i>Mitchella repens</i>	MIRE	0.09 (0.07) <i>a</i>	0.02 (0.02) <i>a</i>
<i>Monotropa uniflora</i>	MOUN3	0.03 (0.02) <i>a</i>	0.05 (0.03) <i>a</i>
<i>Galearis spectabilis</i>	GASP5	0.02 (0.02)	–
<i>Osmorhiza claytoni</i>	OSCL	0.52 (0.19) <i>a</i>	0.11 (0.07) <i>a</i>

TABLE 4 (Cont.)

Ground-flora mean cover values and richness for north-facing and south-facing old-growth ecosystems in southeastern Ohio. Values are means \pm 1 SE. Values in a row followed by the same letter are not significantly different at $P < 0.05$ (Mann-Whitney test).

Species Name	Code	Mean Cover	
		North-Facing	South-Facing
<i>Dichanthelium boscii</i>	DIBO2	–	0.03 (0.02)
<i>Dichanthelium commutatum</i>	DICO2	–	0.13 (0.09)
<i>Dichanthelium dichotomum</i> var. <i>dichotomum</i>	DIDID	–	0.11 (0.06)
<i>Parthenocissus quinquefolia</i>	PAQU2	1.08 (0.26) <i>a</i>	0.78 (0.23) <i>a</i>
<i>Phlox divaricata</i>	PHDI5	0.05 (0.03) <i>a</i>	0.03 (0.03) <i>a</i>
<i>Pilea pumila</i>	PIPU2	0.38 (0.20) <i>a</i>	0.02 (0.02) <i>a</i>
<i>Polysticum acrostichoides</i>	POAC4	0.28 (0.17) <i>a</i>	0.33 (0.17) <i>a</i>
<i>Polygonatum biflorum</i>	POBI2	0.23 (0.09) <i>a</i>	0.22 (0.06) <i>a</i>
<i>Poa cuspidata</i>	POCU4	0.14 (0.09) <i>a</i>	0.45 (0.14) <i>a</i>
<i>Podophyllum peltatum</i>	POPE	0.14 (0.09) <i>a</i>	0.05 (0.03) <i>a</i>
<i>Potentilla simplex</i>	POSI2	0.02 (0.02) <i>a</i>	0.33 (0.20) <i>a</i>
<i>Porteranthus stipulatus</i>	POST5	–	0.06 (0.06)
<i>Polygonum virginianum</i>	POVI2	0.25 (0.12)	–
<i>Rosa carolina</i>	ROCA4	–	0.14 (0.06)
<i>Sanicula canadensis</i>	SACA15	0.05 (0.03) <i>a</i>	0.08 (0.05) <i>a</i>
<i>Sanicula marilandica</i>	SAMA2	0.02 (0.02)	–
<i>Sanicula trifoliata</i>	SATR4	0.25 (0.13)	–
<i>Sedum ternatum</i>	SETE3	0.09 (0.05) <i>a</i>	0.05 (0.05) <i>a</i>
<i>Smilax glauca</i>	SMGL	0.02 (0.02) <i>a</i>	0.23 (0.08) <i>a</i>
<i>Smilax tamnoides</i>	SMTA2	0.06 (0.04)	–
<i>Maianthemum racemosum</i> ssp. <i>racemosum</i>	MARAR	0.20 (0.13) <i>a</i>	0.30 (0.09) <i>a</i>
<i>Smilax rotundifolia</i>	SMRO	–	0.80 (0.19)
<i>Solidago caesia</i>	SOCA4	–	0.44 (0.14)
<i>Toxicodendron radicans</i>	TORA2	0.22 (0.11) <i>a</i>	0.03 (0.02) <i>a</i>
<i>Uvularia perfoliata</i>	UVPE	0.08 (0.05) <i>a</i>	0.03 (0.03) <i>a</i>
<i>Vaccinium pallidum</i>	VAPA4	–	0.50 (0.27)
<i>Viburnum acerifolium</i>	VIAC	1.03 (0.34) <i>a</i>	1.53 (0.30) <i>a</i>
<i>Vitis aestivalis</i>	VIAE	0.22 (0.10) <i>a</i>	0.28 (0.12) <i>a</i>
<i>Viola palmata</i>	VIPA3	0.11 (0.04) <i>a</i>	0.22 (0.07) <i>a</i>
<i>Viburnum prunifolium</i>	VIPR	0.13 (0.10) <i>a</i>	0.05 (0.03) <i>a</i>
<i>Viola pubescens</i>	VIPU3	0.33 (0.20)	–
Structural Characteristics			
Total mean cover		11.2 (1.2) <i>a</i>	8.9 (1.2) <i>a</i>
Richness (no. of species)		19.6 (1.7) <i>a</i>	20.4 (1.7) <i>a</i>

highly variable between the old-growth ecosystem types. Mid-diameter of fallen trees is similar, averaging (\pm 1 SE) 18.5 (1.5) cm in the north-facing old-growth stands, and 17.2 (2.1) cm in the south-facing old-growth stands ($P > 0.05$). Whereas snag density tends to be higher in the

south-facing old-growth ecosystem, fallen tree density tends to be higher in the north-facing ecosystem ($P < 0.10$). Volume of fallen trees is also significantly different ($P < 0.05$), with higher volumes in the north-facing stands than the south-facing stands (Fig. 4).

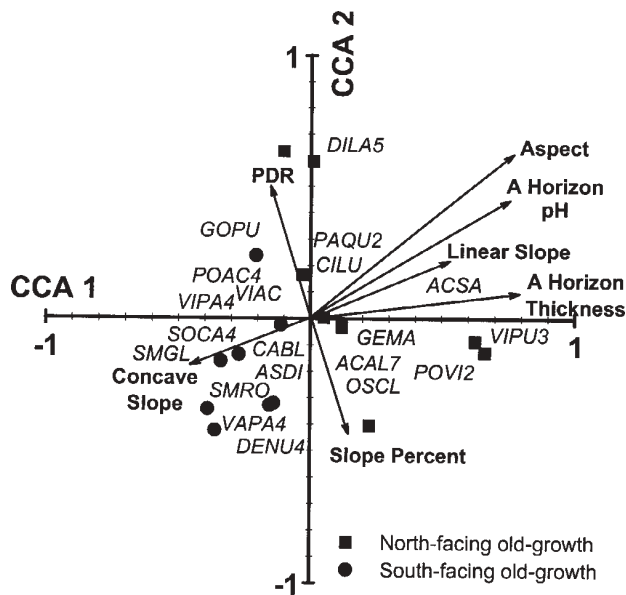


FIGURE 2. Ground-flora canonical correspondence analysis (CCA) triplot of old-growth ecosystems in southeastern Ohio. (See Table 4 for species acronym codes.)

DISCUSSION

Most studies of old-growth forests in eastern North America have focused on individual tracts instead of taking an ecosystem approach to characterize the composition and structure of old-growth forest ecosystem types (for example, Roovers and Shifley 1997). As a result, our knowledge and understanding of the composition, structure, and function of eastern old-growth has primarily been obtained by studying old-growth remnants. Furthermore, the composition and structure of current second-growth stands have been compared to those of remnant old-growth stands to determine the successional status of the second-growth stands (Hale and others 1999), as well as guiding any

forest management practices designed to emulate old-growth conditions. This can be problematic for forest ecosystem restoration as these individual old-growth remnants are often used as 'blueprints' for restoration (Frelich and Puettmann 1999), and do not adequately represent the inherent variability in these forest ecosystems. Consequently, research that is focused on developing reference conditions for forest ecosystem restoration should focus on developing composite descriptions based on measurements taken from several locations rather than a single site or old-growth remnant (SER 2002). Our landscape ecosystem approach provides us with such an opportunity to develop a suite of composite reference conditions for old-growth ecosystem types. Additionally, our utilization of the Wayne National Forest ecosystem classification system (which was based on mature second-growth forests) provides us with a framework with which to compare the ecological properties of these contrasting old-growth ecosystem types rather than merely summarizing the characteristics of a single stand of old trees or old-growth remnant.

In southeastern Ohio, the stand structure is relatively similar between north-facing and south-facing old-growth forest ecosystem types. Our results suggest that these forest ecosystem types have 15 to 16 different overstory species, approximately 30 m²/ha of basal area, and densities between 322 and 360 trees/ha. However, the old-growth north-facing middle slope ecosystem types are dominated by overstories of mesic species, including sugar maple, northern red oak, and American beech while old-growth south-facing ecosystem types are dominated by mixed-oaks. Similar trends, that is, different composition but similar structure, are also observed with the coarse woody debris in these ecosystem types. However, there appears to be considerable variability in the coarse woody debris both within and between ecosystem types.

Corresponding to differences in A-horizon characteristics, the ground-flora composition of the old-growth ecosystem type located on north-facing slopes is dominated by a rich community of mesic perennials, including *Actaea pachypoda* Ell., *Circaea lutetiana* L., *Osmorhiza claytoni* (Michx.) C.B. Clarke, *Viola pubescens* Ait., and *Polygonum virginianum* L. Different species, including *Smilax rotundifolia* L., *Solidago caesia* L., *Carex blanda* Dewey, and *Desmodium nudiflorum* (L.) DC., characterize the south-facing old-growth ecosystem type. These species include a mixture of xeric woody vines and shrubs, perennials, and graminoids. Contrary to what we would have anticipated based on the edaphic difference observed between these two forest ecosystem types, ground-flora species richness and total cover are similar.

As demonstrated here, quantifying the differences in composition and structure of different old-growth ecosystem types rather than individual old-growth remnants is the first step in effectively managing the remaining and future old-growth forests of the Central Hardwoods Region (Sauer 1998). By focusing on the interrelationships between local ecosystem components,

TABLE 5

Relative density of coarse woody debris (CWD) between south-facing and north-facing old-growth ecosystems of southeastern Ohio.

Genus	North-facing	South-facing
Standing Snags		
<i>Quercus</i>	28.0	68.0
<i>Carya</i>	8.0	11.0
<i>Acer</i>	56.0	5.0
<i>Fagus</i>	0.0	5.0
Other	8.0	11.0
Fallen Trees		
<i>Quercus</i>	31.0	84.0
<i>Carya</i>	1.0	2.0
<i>Acer</i>	11.0	7.0
<i>Fagus</i>	0.0	0.0
Other	57.0	7.0

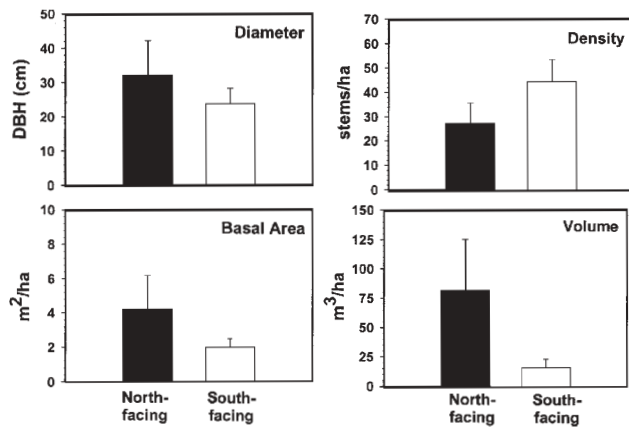


FIGURE 3. Snag characteristics of north-facing and south-facing old-growth ecosystems in southeastern Ohio.

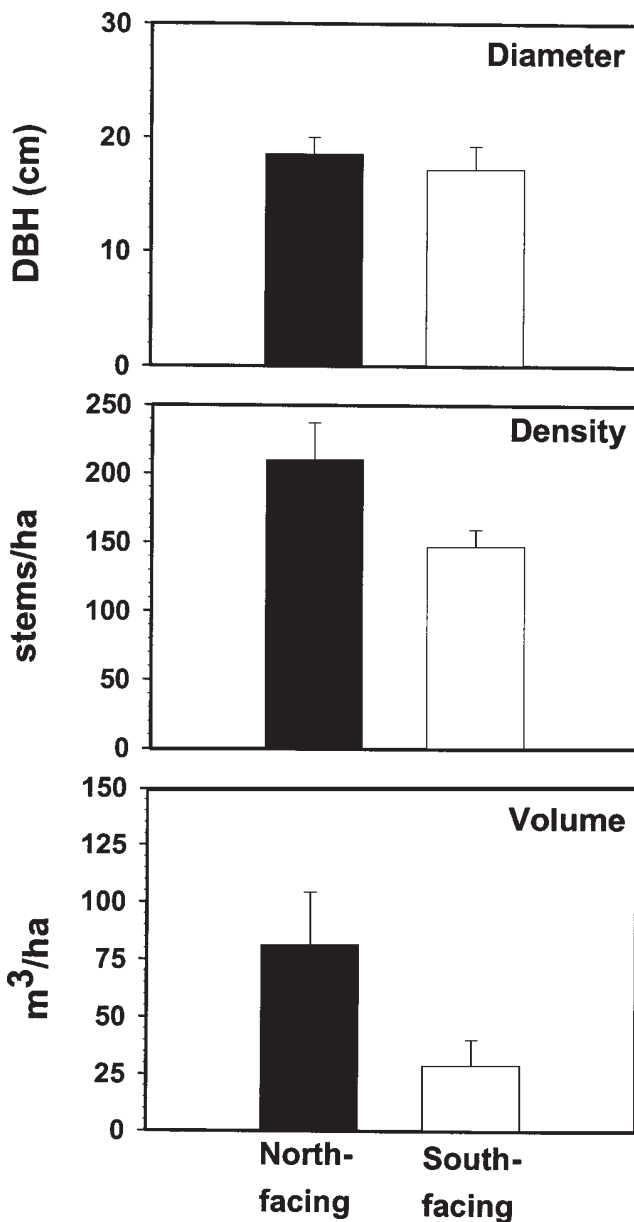


FIGURE 4. Coarse woody debris (CWD) characteristics of north-facing and south-facing old-growth ecosystems in southeastern Ohio.

such as the influence of physiography and soils on the composition and structure of old-growth plant communities, a better understanding of the old-growth processes will surely follow. Additionally, we can begin to quantify the variation in different compositional and structural components of these forest ecosystem types, an important first-step in forest ecosystem restoration (Palmer and others 1997), as well as develop management practices that emulate the natural disturbance regimes that influence the composition and structure of forest ecosystems (Palik and others 2002). The end result will lead to the improvement of functional definitions of eastern old-growth forest ecosystems, and ultimately advance our ability to effectively restore and manage them.

ACKNOWLEDGMENTS. We gratefully acknowledge financial support from the USDA Forest Service to help conduct this research. Additional salaries and research support were provided from State and Federal funds appropriated to the Ohio Agricultural Research and Development Center (OARDC). We especially thank the support of Adele Olivero; without her work this study could not have been completed. Assistance in locating study areas was provided by Philip Cantino and Marilyn Ort. We sincerely thank the cooperating landowners for permission to conduct this study, as well as two anonymous reviewers who provided many useful editorial comments.

LITERATURE CITED

- Barnes BV. 1989. Old-growth forests of the northern Lake States: a landscape ecosystem perspective. *Natural Areas J* 9:45-57.
- Barnes BV, Zak DR, Denton SR, Spurr SH. 1998. *Forest Ecology*, 4th ed. New York (NY): J Wiley. 774 p.
- Cho DS, Boerner REJ. 1991. Canopy disturbance patterns and regeneration of *Quercus* species in two old-growth forests. *Vegetatio* 93:9-18.
- Frellich LE, Puettmann K. 1999. Restoration Ecology. In: Hunter ML Jr, editor. *Maintaining Biodiversity in Forest Ecosystems*. Cambridge (UK): Cambridge Univ Pr. p 498-524.
- Goebel PC, Hix DM. 1996. Development of mixed-oak forests in southeastern Ohio: a comparison of second-growth and old-growth forests. *Forest Ecol and Mgmt* 84:1-21.
- Goebel PC, Hix DM. 1997. Changes in the composition and structure of mixed-oak, second-growth forest ecosystems during the understory reinitiation stage of stand development. *Écoscience* 4:327-39.
- Hale CM, Pastor J, Rusterholz KA. 1999. Comparison of structural and compositional characteristics in old-growth and mature, managed hardwood forests of Minnesota, U.S.A. *Canadian J of Forest Research* 29:1479-89.
- Hix DM, Pearcy JN. 1997. Forest ecosystems of the Marietta Unit, Wayne National Forest, southeastern Ohio: multifactor classification and analysis. *Canadian J of Forest Research* 27:1117-31.
- Hix DM, Pearcy JN, McClenahan JR. 1997. Development of an ecological classification system for the Wayne National Forest: final technical report. Report to the USDA Forest Service, Columbus, OH: The Ohio State Univ, School of Natural Resources. 131 p.
- Kent M, Coker P. 1992. *Vegetation Description and Analysis: A Practical Approach*. London: Bellhaven Pr. 363 p.
- Keys J Jr, Carpenter C, Hooks S, Koenig F, McNab WH, Russell W, Smith ML. 1995. *Ecological units of the Eastern United States – first approximation*. Atlanta (GA): US Dept of Agriculture, Forest Serv. 83 p.
- Leverett R. 1996. Definitions and history. In: Davis MB, editor. *Eastern Old-Growth Forests: Prospects for Rediscovery and Recovery*. Washington (DC): Island Pr. p 3-17.
- Lucht TE, Brown DL, Martin NH. 1985. *Soil Survey of Athens County*. USDA and Ohio Dept of Nat Resources. 192 p.
- McCarthy BC, Hammer C, Kauffman G, Cantino P. 1987. Vegetation patterns and structure of an old-growth forest in southeastern Ohio. *Bull Torrey Bot Club* 114:33-45.
- McCarthy BC, Small CJ, Rubino DL. 2001. Composition, structure and dynamics of Dysart Woods, an old-growth mixed mesophytic

- forest of southeastern Ohio. *Forest Ecol and Mgmt* 140:193-213.
- McLean EO. 1982. Soil pH and lime requirement. In: Page AL, editor. *Methods of Soil Analysis, Part 2. Agronomy Monograph No. 2.* Madison (WI): American Society of Agronomy. p 199-223.
- Meier AJ, Bratton SP, Duffy DC. 1996. Biodiversity in the herbaceous layer and salamanders in Appalachian primary forests. In: Davis MB, editor. *Eastern Old-Growth Forests: Prospects for Rediscovery and Recovery.* Washington (DC): Island Pr. p 49-64.
- Olivero AM, Hix DM. 1998. Influence of aspect and stand age on ground flora of southeastern Ohio forest ecosystems. *Plant Ecol* 139:177-87.
- Palik BJ, Goebel PC, Kirkman LK, West L. 2000. Using landscape hierarchies to guide restoration of disturbed ecosystems. *Ecological Applications* 10:189-202.
- Palik BJ, Mitchell RJ, Heirs JK. 2002. Modeling silviculture after natural disturbance to sustain biodiversity in the longleaf pine (*Pinus palustris*) ecosystem: balancing complexity and implementation. *Forest Ecol and Mgmt* 155:347-56.
- Palmer MA, Ambrose RF, Poff NL. 1997. Ecological theory and community restoration ecology. *Restoration Ecol* 5:291-300.
- Parker GR. 1989. Old-growth forests of the Central Hardwood Region. *Natural Areas J* 9:5-11.
- Pickett STA, Parker TV. 1994. Avoiding the old pitfalls: opportunities in a new discipline. *Restoration Ecol* 2:75-9.
- Pregitzer KS, Goebel PC, Wigley TB. 2001. Evaluating forestland classification schemes as tools for the maintenance of biodiversity. *J of Forestry* 99:33-40.
- Roovers LM, Shifley SR. 1997. Composition and dynamics of Spitzer Woods, an old-growth remnant forest in Illinois (USA). *Natural Areas J* 17:219-32.
- Rowe JS, Barnes BV. 1994. Geo-ecosystems and bio-ecosystems. *Bull of the Ecological Soc of Amer* 75:40-1.
- Rowe JS, Sheard JW. 1981. Ecological classification: a survey approach. *Environ Mgmt* 5:451-64.
- Rypma RB. 1961. The structure and pattern of the primary forests of Athens and Washington counties, Ohio [dissertation]. Columbus (OH): The Ohio State Univ. 173 p.
- Sauer LJ. 1998. The once and future forest: a guide to forest restoration. Washington (DC): Island Pr. 381 p.
- [SER] Society for Ecological Restoration Science and Policy Working Group. 2002. The SER Primer on Ecological Restoration. www.ser.org/.
- Smith DM. 1986. *The Practice of Silviculture*, 8th edition. New York: John Wiley. 527 p.
- ter Braak CJF, Smilauer P. 1998. CANOCO reference manual and user's guide to CANOCO for Windows: software for canonical community ordination (version 4.0). Ithaca (NY): Microcomputer Power.
- Trombulak SC. 1996. The restoration of old-growth; why and how. In: Davis MB, editor. *Eastern Old-Growth Forests: Prospects for Rediscovery and Recovery.* Washington (DC): Island Pr. p 305-20.