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Characteristics of Mixed-Oak Forest Ecosystems in Southern Ohio Prior to the Reintroduction of Fire

Abstract

Mixed-oak forests occupied much of the Unglaciated Allegheny Plateau region of southern Ohio at the onset of Euro-American settlement (ca. 1800). Historically, Native Americans used fire to manage the landscape and fire was frequent throughout the 19th and early 20th centuries during extensive forest harvesting and then re-growth. Today, though mixed-oak forests remain dominant across much of the region, oak regeneration is often poor as other tree species (e.g., maples) are becoming much more abundant. This shift has occurred concurrently with fire suppression policies that began in 1923. A multidisciplinary experiment was initiated in southern Ohio to explore the use of prescribed fire as a tool to improve the sustainability of mixed-oak forests. This report describes the experimental design and study areas, and provides baseline data on ecosystem characteristics prior to prescribed fire treatments. Chapters describe forest history, an integrated moisture index, geology and soils, understory light environments, understory vegetation, tree regeneration, overstory vegetation, foliar nutrient status, arthropods, and breeding birds.

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Characteristics of Mixed-Oak Forest Ecosystems in Southern Ohio Prior to the Reintroduction of Fire

Edited by Elaine Kennedy Sutherland and Todd F. Hutchinson

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Contents

Chapter 1 1
Introduction, Study Area Description, and Experimental Design
Elaine Kennedy Sutherland, Todd F. Hutchinson, and Daniel A. Yaussy

Chapter 2 17
History of Forests and Land-use
Todd F. Hutchinson, Darrin Rubino, Brian C. McCarthy, and Elaine Kennedy Sutherland

Chapter 3 29
A GIS-Derived Integrated Moisture Index
Louis R. Iverson and Anantha M. Prasad

Chapter 4 43
Physiography, Geology, and Soil Classification
Ralph E. J. Boerner and Elaine Kennedy Sutherland

Chapter 5 47
Soil and Forest Floor Characteristics
Ralph E. J. Boerner, Sherri J. Morris, Kelly L. M. Decker, and Todd F. Hutchinson

Chapter 6 57
Canopy Openness, Understory Light Environments, and Oak Regeneration
Brian C. McCarthy and Scott A. Robison

Chapter 7 67
Understory Vegetation
Steve Sutherland, Todd F. Hutchinson, and Jennifer L. Windus

Chapter 8 85
Composition and Abundance of Tree Regeneration
Todd F. Hutchinson, Elaine Kennedy Sutherland, and Charles T. Scott

Chapter 9 99
Structure, Composition, and Condition of Overstory Trees
Daniel A. Yaussy, Todd F. Hutchinson, and Elaine Kennedy Sutherland

Chapter 10 113
Foliar Nutrient Concentrations of Oak, Hickory, and Red Maple
Amy J. Scherzer, Robert P. Long, and Joanne Rebbeck

Chapter 11 123
Monitoring Selected Arthropods
R. Chris Stanton, David J. Horn, Foster F. Purrington, John W. Peacock, and Eric H. Metzler

Chapter 12 139
Breeding Bird Communities
Vanessa L. Artman and Randy Dettmers

Appendix 157
Publications resulting from the research project described in this volume.

Chapter 1

Introduction, Study Area Description, and Experimental Design

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Abstract

Throughout much of the Eastern Deciduous Forest, the sustainability of oak-dominated forests is threatened by poor oak regeneration as other tree species increase in abundance. Historically, fire was a frequent process in oak-dominated ecosystems (savannas, woodlands, open-structured forests) as Native Americans and then Euro-American settlers used fire for a variety of purposes. Oaks are well adapted to fire and aggressive fire suppression since ca. 1930 is considered a key factor contributing to the reduced sustainability of oak ecosystems today. As forests become more dense and oak abundance decreases, species adapted to open-structured forests and dependent on hard-mast will likely be affected as well. In 1994, we initiated a multidisciplinary study of prescribed fire as a tool to restore structure, composition, and function to mixed-oak forest ecosystems in southern Ohio. In this chapter we introduce the problem and the rationale for the study. We also describe the experimental design and general characteristics of the climate, physiography, land-use history, fire regimes, and forests of the study areas.

Introduction

Sustainability of Oak Forest Ecosystems

The most abundant forest type in the United States is oak-hickory (Smith et al. 2001). However, in historically oak-dominated landscapes throughout the eastern deciduous forest, tree species other than oak, including red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), blackgum (*Nyssa sylvatica*) yellow poplar (*Liriodendron tulipifera*), and beech (*Fagus grandifolia*), are increasing in abundance (Abrams 1992). The advance reproduction of closed canopy oak stands and the re-growth following canopy disturbance are often dominated by these species.

Written accounts prior to Euro-American settlement often described open-structured oak forests and the use of fire by Native Americans (Whitney 1994; Bonnickson 2000). The long-term abundance of oak in eastern deciduous forests has been associated with fire, as evidenced by palynology studies of charcoal and oak pollen from lake sediments (Clark and Royall 1995; Delcourt and Delcourt 1997; Maenza-Gmelch 1997; Delcourt et al. 1998; Fuller et al. 1998). Studies of fire-scarred trees indicate frequent fire (return intervals less than 10 years) in oak forests and woodlands before and after Euro-American settlement, until organized fire suppression began, ca. 1930 (Guyette and Cutter 1991; Cutter and Guyette 1994; Sutherland 1997; Shumway et al. 2001). Aggressive fire suppression over the last 70 years is widely considered to be the most important factor contributing to the reduced sustainability of oak-dominated forests today (Lorimer 1984; Abrams 1992; Lorimer 1993; Van Lear and Watt 1993).

Oaks possess a suite of physical adaptations that render them both resistant and resilient to fire, thus likely improving their competitive status in a disturbance regime characterized by frequent surface fires (Van Lear and Watt 1993). Oak seedlings and sprouts are highly resilient to top-killing; the large rootstocks can remain viable and continue to sprout after repeated fires. Larger oak trees have thick bark, limiting damage to cambial tissue during fire (Hengst and Dawson 1994). When fire-caused wounding does occur, damage is rapidly compartmentalized (Smith and Sutherland 1999). Van Lear and Watt (1993) and Wade et al. (2000) summarized the functional role of fire in the ecology of oak regeneration: fire creates optimal seedbeds and encourages seed caching; fire reduces acorn and seedling predators; fire reduces the abundance of fire-sensitive competitors, thus increasing light availability for oak seedling growth; fire dries soils, favoring oaks over more

mesic species; fire promotes the production of fine fuels (grasses and forbs) that increases the probability of future fires. Frequent long-term burning can also reduce nitrogen availability, which should favor oaks over more nutrient-demanding species, e.g., sugar maple and beech (Boerner et al. 1988; Eivasi and Bryan 1996).

In contrast, species that are increasing in abundance in oak forests possess traits that suggest a competitive disadvantage in a regime of frequent fire, including thin-bark (red maple, beech, yellow poplar), high degree of shade tolerance (sugar maple, red maple, blackgum, beech), and high shoot-to-root ratio (red maple, yellow poplar). In southern Ohio, all of these species were common historically only on mesic to hydric landscape positions, including lower north-facing slopes, ravines, and larger bottomlands; areas that likely burned less frequently and intensely (Dyer 2001).

Reduced oak abundance has many ramifications. Historically, oaks have been dominant components of the region's forests for millenia (Delcourt and Delcourt 1991; Abrams 2002). As oak forests shift in structure and composition, other ecosystem components likely will be affected. In mixed-mesophytic forests, with oak as a component, tree diversity has been shown to decrease with increasing sugar maple dominance (Schuler and Gillespie 2000). Midwestern oak savannas and woodlands maintained with fire contain highly diverse plant communities, often harboring threatened and endangered species (Taft et al. 1995; Anderson et al. 1999; Leach and Givnish 1999). As oak woodlands and forests become more dense with shade-tolerant trees, plant diversity may decline with the loss of species adapted to frequent disturbance and more open conditions. For example, in tallgrass prairie, the removal of fire from the landscape can cause significant plant species' loss (Leach and Givnish 1996).

Also, the hard mast produced in oak-hickory forests is consumed by numerous species of mammals and birds and thus a major contributing factor to community functioning (McShea 2000; McShea and Healy 2002). In the eastern U.S., bird species adapted to open habitats maintained by disturbance (grasslands, savannas, woodlands, open-structured forests) are declining at higher rates than species adapted to closed-canopied forests (Brawn et al. 2001; Hunter et al. 2001). In the central hardwoods region, declining species that are adapted to open-structured forests include the cerulean warbler (*Dendroica cerulea*), red-headed woodpecker (*Melanerpes erythrocephalus*), and eastern wood-pewee (*Contopus virens*) (Hunter et al. 2001). Oak-dominated forests also have been shown to support a greater abundance of birds than maple-dominated forests (Rodewald and Abrams 2002). In addition to bird species dependent on acorns, e.g., red-bellied woodpecker (*Melanerpes carolinus*), and tufted titmouse (*Baeolophus bicolor*), the bark and foliage structure of oaks may provide better foraging for bark- and foliage-gleaning species (Rodewald and Abrams 2002). In addition to these ecological ramifications, economic losses may be significant as well because of the high commercial value of oak lumber.

Forests and Fire in Southern Ohio

Written accounts of the Ohio Valley prior to Euro-American settlement described park-like forests ("open woods", "clear woods") and the frequent use of fire by Native Americans in some areas for the purposes of hunting and landscape management (Chapter 2). However, specific fire regimes in the presettlement landscape are poorly understood.

At the onset of Euro-American settlement (ca. 1795-1805), witness trees recorded for the original land surveys indicated forests dominated by oak covered much of the Unglaciated Allegheny Plateau in southeastern Ohio (Gordon 1969; Dyer 2001). Throughout the 19th century, nearly all forests in southern Ohio were harvested, primarily for agriculture and the production of timber and fuel (Williams 1989).

Dendroecological studies of second-growth oak forests indicate fire return intervals ranging from 5 to 15 years, with fires becoming much less frequent after the establishment of organized fire suppression in 1923 (Sutherland 1997; Sutherland, unpublished data). Fire statistics (ca. 1910-2001) for 10 counties in southern Ohio indicate a steep decline in the annual acreage burned after 1923 (Fig. 1).

Currently, forests cover approximately 55% of the land in southeastern Ohio with 68% of the forestland classified as oak-hickory (Griffith et al. 1993). However, from 1968 to 1991, oak and hickory volume have declined relative to that of maple, black cherry, and yellow poplar (Chapter 3). Mature secondary forests have densities of 350 to 400 trees per hectare (Chapter 9). From land surveys in southern Illinois, Anderson and Anderson (1975) estimated an average density of only 160 trees per hectare for presettlement oak-hickory forests, forests similar in composition to the presettlement forests of southern Ohio (Chapter 2).

Similar to regional trends, the density of oak advance reproduction (large seedlings and saplings) is likely inadequate for successful oak regeneration after disturbance (Goebel and Hix 1997; Chapter 8). Indeed,

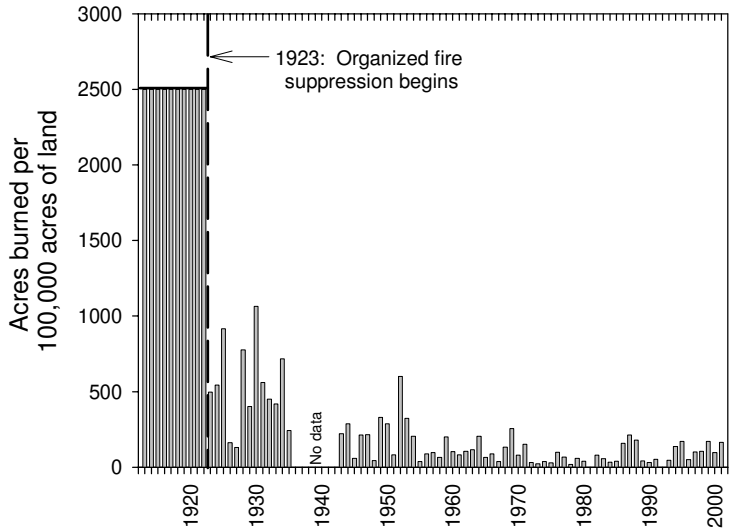

Figure 1.-- The annual acreage burned per 100,000 acres of land for 10 counties (Adams, Athens, Gallia, Hocking, Jackson, Lawrence, Pike, Ross, Scioto, Vinton) in southeastern Ohio. The 1913-1922 annual value is based on an estimate that 333,546 acres (of 1.3 million total forest acres) had burned within the previous 10 years. The estimate is from a 1920-1922 forest survey of the 10 counties and is contained in a 1931 Ohio Division of Forestry unpublished report titled "Forest fire control plan for Ohio". The 1923-1935 data are from Leete (1938). All other fire statistics (1943-2001) are from Ohio Division of Forestry records.

following timber harvest, the relative abundance of oak has been shown to decrease significantly, particularly on mesic sites. (Heiligman et al. 1985; Norland and Hix 1996; Iverson et al. 1997).

Objectives of the Ecosystem Management Study: Effectiveness of Prescribed Burning in the Ecological Restoration of Mixed-Oak Forest Ecosystems

On many public forestlands, management has shifted towards an ecosystem management approach. The main objective of ecosystem management is to sustain ecosystem composition, structure, and function by applying sound ecological knowledge (Christensen et al. 1996). For ecosystems that have shifted away from desired conditions, restoration is often a key component of ecosystem management. Ecological restoration is an elusive goal. Restoration often focuses on a historical reference point, such as the conditions encountered prior to Euro-American settlement (Stephenson 1999). Restoring composition often requires the restoration of processes, such as disturbance regimes and resource supply rates.

In southern Ohio, forest structure and composition almost certainly varied considerably in past millennia, in response to climatic variation and human land use. Landscapes cannot be fully restored to the presettlement conditions of the late 18th century, after extensive harvesting, introduced tree diseases (e.g., chestnut blight), and the extirpation of animal species (e.g., the timber wolf, woodland bison, passenger pigeon). However, given the evidence that fire has played an important role in the development and maintenance of oak-dominated ecosystems, we initiated a large-scale study of prescribed fire as a restoration tool in mixed-oak forests.

For this study, the desired future condition is a more open-structured and more functionally sustainable mixed-oak forest ecosystem. We hypothesize that frequent fires of low to moderate intensity will alter forest structure, composition, and function, enhancing the regeneration potential of oak while also promoting species adapted to open-structured forests in which fire is a frequent disturbance process. The frequency and intensity of fire will be directly related to the degree of change in plant and animal communities.

The application of any management tool on public lands, particularly Federal lands, requires supporting documentation concerning potential effects on the ecosystem (Christensen et al. 1996; Thomas 1996). To aid in the management of oak-dominated ecosystems, our objective is to provide land managers with quantitative information on how fire affects sustainability, biodiversity, and ecosystem functioning.

In this chapter, we describe the study areas and experimental design. As Sheriff and He (1997) stated, manipulative experiments must include defined treatments, randomization, and replication to infer cause-and-effect relationships. The study includes pretreatment monitoring of conditions on all sites as well as unburned control areas and will include monitoring of the following ecosystem components:

- Overstory: structure, composition, productivity, foliar nutrient status.
- Tree regeneration: structure and composition.
- Understory vegetation: composition and diversity, threatened and endangered species.
- Light availability: canopy openness and light environment.

Table 1.--General characteristics of the four study areas. Values for slope, stand age, tree basal area and oak basal area are means (+/- 1 SE) from the 27 vegetation plots in each study area.

Study Area County Latitude, Longitude	Area (ha)	Elevational range (m)	Percent slope	Primary soil series	Stand age (years)	Tree basal area (m^2/ha)	Oak basal area (%)
Watch Rock Vinton County 39°12' N, 82°23' W	76.8	210-281	29.2 (2.5)	Steinsburg-Gilpin Association	112 (4.6)	25.3 (0.7)	68.9 (4.5)
Arch Rock Vinton County 39°11' N, 82°22' W	80.1	214-266	33.4 (2.3)	Steinsburg-Gilpin Association	108 (2.1)	27.2 (0.7)	72.5 (4.3)
Young's Branch Lawrence County 38°43' N, 82°41' W	75.3	242-298	31.6 (1.2)	Steinsburg-Shelocta Association	121 (5.3)	27.8 (0.8)	67.1 (4.3)
Bluegrass Ridge Lawrence County 38°36' N, 82°31' W	109.3[1]	222-295	23.7 (1.0)	Upshur-Gilpin-Steinsburg Association	100 (3.9)	27.1 (0.9)	70.0 (5.9)

[1]Includes an area of approximately 10 ha in the infrequent burn unit that was clearcut within the last 20 years and thus was not included in the study.

- Belowground: soil nutrient status and cycling rates; organic matter quantity and turnover; abundance and activity of key soil microbial groups.
- Fauna: community composition, diversity, and functioning, with emphasis on breeding birds and arthropods.

Experimental Design and Study Area Description

The study was designed to test the effects of prescribed fire on various ecosystem components at five separate study areas. The dissected topography of southern Ohio causes significant variability in microclimate and soil moisture across the landscape, which in turn affects vegetation structure and composition. A split-plot design was thus established to incorporate soil moisture as a factor. The study areas are replicate blocks, fire treatment is the whole plot factor, and soil moisture class the subplot factor.

Study Areas

In cooperation with our management partners, MeadWestvaco Corporation and The Wayne National Forest, a pool of potential study areas was selected based on the following criteria: 1) areas have been continuously forested, historically (forests on abandoned agricultural lands were excluded); 2) areas have at least 75 ha of contiguous land to delineate three separate treatment units of 25 ha for adequate monitoring of avian populations (Chapter 12); 3) stands within the areas are at least 80 years of age, in the understory reinitiation stage of stand development (Oliver and Larson 1996); 4) areas contain adequate land modeled as xeric, intermediate, and mesic in soil moisture (described below); 5) oak is a major component of the overstory in all moisture classes; and 6) parent materials are sandstones and shales that produce the relatively acidic, well-drained soils typical of the unglaciated Allegheny Plateau.

After field reconnaissance, the five most-suitable study areas were selected, two in Vinton County (Arch Rock and Watch Rock) and three in Lawrence County (Young's Branch, Bluegrass Ridge, and Sharp's Creek). However, pilot data indicated that soil pH and fertility were much greater in some portions of Bluegrass Ridge and Sharp's Creek, which contained significant interbedded limestone. Because of the close proximity of the two areas, we selected three (two at Bluegrass Ridge; one at Sharp's Creek) of the six units that were most similar to the other study areas in soil chemistry to combine into one study area (Bluegrass Ridge), eliminating the other three units and resulting in four study areas.

Watch Rock and Arch Rock are located in the Raccoon Ecological Management Area (REMA), a 6,900 ha tract

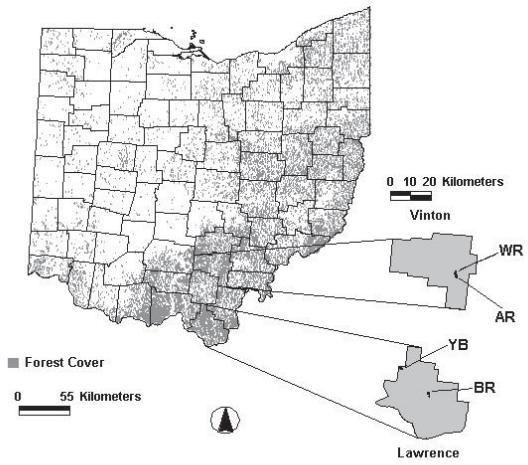

Figure 2.--Map of Ohio showing the location of the four study areas in Vinton and Lawrence Counties. WR = Watch Rock, AR = Arch Rock, YB = Young's Branch, BR = Bluegrass Ridge.

of contiguous forest owned by MeadWestvaco Corporation (Fig. 2). Young's Branch and Bluegrass Ridge are located in the Ironton District of the Wayne National Forest. In general, the terrain, soils, and forests are similar among the four study areas (Table 1).

The study areas are located in the Southern Unglaciated Allegheny Plateau Section of the Eastern Broadleaf Forest Province, which is characterized as a maturely dissected plateau of high hills, sharp ridges and narrow valleys (McNab and Avers 1994). The sites are underlain predominantly by sandstones and shales of Pennsylvanian age and soils are mostly loams and silt loams that are acidic and well-drained. Physiography, geology and soils are described in Chapters 4 and 5.

Lawrence County is slightly warmer and wetter than Vinton County with a mean annual temperature difference of 1.6 ºC and a mean annual precipitation difference of 35 mm (Fig. 3). Also, Lawrence County averages 27 more frost-free days than Vinton County. Both counties always attain freezing temperatures in April and sometimes in May. The first date of freezing temperatures in fall occurs between September and November in both counties. Moderate to severe droughts (Palmer Drought Severity Indices of -2 to –3) have occurred infrequently since 1930. It should be noted that for Lawrence County, all weather stations were located along the Ohio River. Thus, these data likely describe more moderate weather conditions than the uplands where the two study areas are located. Given the dissected topography common in this landscape, microclimate variation at the local scale (within study areas) is greater than macroclimate variation at the regional scale (among study areas).

The species composition of presettlement forests and the subsequent land use history of the study areas are similar to many forested uplands in southern Ohio. Witness trees recorded for the original land surveys (ca. 1795-1805) indicate that forests were oak-dominated, with white oak (*Quercus alba*) the most abundant species (Chapter 2). Vinton and Lawrence Counties remained largely forested until the rise of the charcoal iron industry (ca. 1830-1860). Iron furnaces were established near each study area and the forests were clearcut for charcoal until the industry declined in the late-1800s (Chapter 2). Forests have since been relatively undisturbed; stand-level disturbances are interpreted with dendroecological methods in Chapter 2. Presently, the most abundant species in the overstory (trees > 10 cm diameter at breast height) are white oak, red maple, chestnut oak (*Q. prinus*), hickories (*Carya* spp.), sugar maple, and black oak (*Q. velutina*) (Chapter 9).

Fire Regimes and Fire Treatments

Though lighting-caused fires do occur in the central hardwoods region (Haines et al. 1975; Ruffner 1998), the great majority of fires are human-caused (Yaussy and Sutherland 1994). Despite human-caused ignitions, seasonal weather patterns dictate the occurrence of fires in southern Ohio (Leete 1938; Yaussy and Sutherland 1994). During spring (March-April) and fall (October-November), weather conditions can cause rapid fuel drying, increasing the probability of fire ignition and spread. The peak of the spring fire season occurs in mid- to late-March in Lawrence County and late-March to early-April in Vinton County (Fig. 4), likely tied to the minor differences in climate. In the winter months, temperatures are generally too low and humidities too high for adequate drying of surface fuels. From leaf expansion (early May) through summer, the forest floor is shaded, covered with lush vegetation, and humidities are high, also reducing the probability of fire propagation. In the Ohio Valley region, fire occurrence is related more strongly to these annual weather cycles than to periodic circulation phenomenon such as the El Nino/Southern Oscillation (Yaussy and Sutherland 1994).

Fires in oak forests are confined to surface fuels such as leaf litter, small woody debris, and understory vegetation (Little 1974; Anderson 1982). Studies of prescribed fire indicate that flame lengths usually are less than 1 m, causing minimal overstory mortality (Brose and Van Lear 1998; Elliot et al. 1999). However, high intensity surface fires can cause significant patches of overstory mortality, particularly when highly flammable tall understory

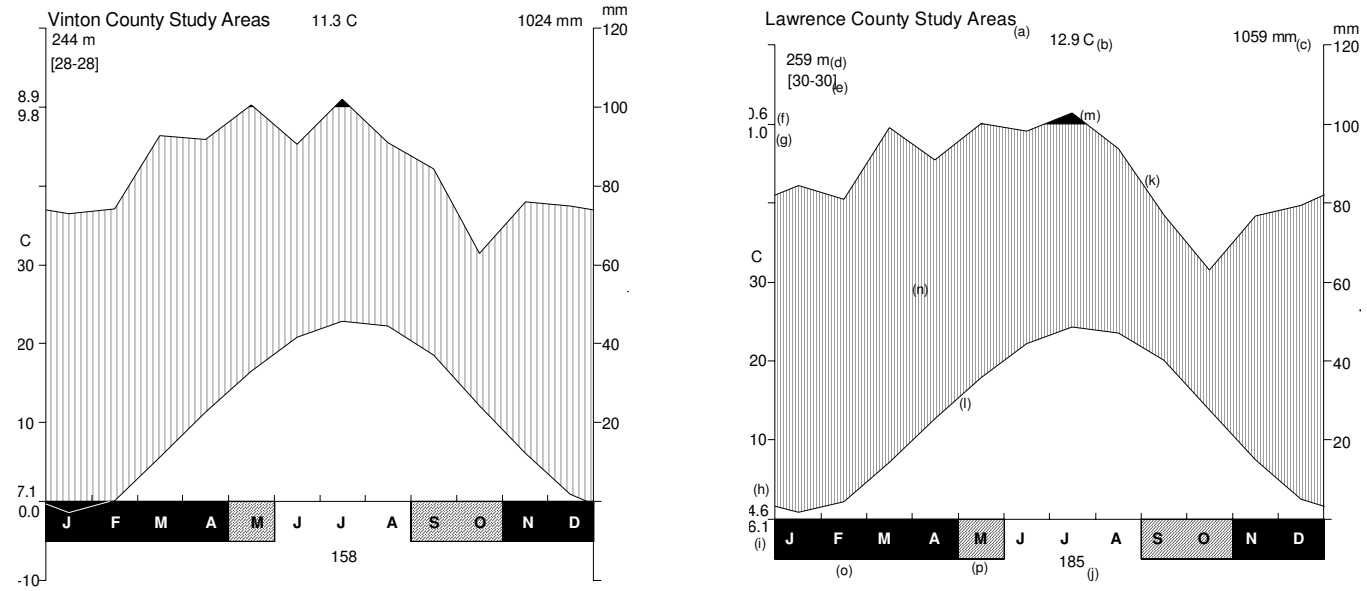

Figure 3.--Climate diagrams for Vinton County and Lawrence county study areas: (a) plot location, (b) mean annual temperature, (c) mean annual precipitation, (d) average elevation of study areas, (e) number of years of record used in computing mean monthly temperature and precipitation respectively, (f) extreme maximum monthly temperature, (g) mean maximum monthly temperature of the warmest month, (h) mean minimum monthly temperature for the coldest month, (i) extreme mean minimum monthly temperature, (j) mean frost-free period, (k) mean monthly precipitation, (l) mean monthly temperature, (m) period when precipitation usually exceeds water holding capacity of soil, (n) period of adequate available moisture, (o) months when temperatures always fell below freezing, (p) months when temperatures sometimes fell below freezing. Data presentation follows Walter (1984).

vegetation (e.g., laurel [*Kalmia*], greenbriar [*Smilax*]) is abundant (Regelbrugge and Smith 1994; Ducey et al. 1996).

For a number of sites in southern Ohio, fire return intervals before the suppression era (ca. 1850-1925) were in the range of 3-7 years (Sutherland 1997; Sutherland, unpublished data). However, the mere imitation of fire regimes that may have sustained mixed-oak forests will not necessarily achieve our objective to alter stand structure. These sites have experienced more than 70 years with little or no fire, during which significant populations of non-oak species have become established in the understory and midstory (Chapters 8 and 9). A single prescribed fire rarely has much effect on the overstory and midstory strata of eastern hardwood communities. Tree species considered susceptible to fire (e.g., yellow-poplar and maples) generally are resistant to fire-caused injury when stems are at least 15 cm in diameter at breast height (d.b.h.), that is, when bark is sufficiently thick to protect the cambium and crowns are sufficiently high to avoid heat-caused injury (Van Lear and Watt 1993). Any attempt to alter forest structure significantly is likely to require multiple fires.

For the initial stage of the project (1995-1999), we chose to evaluate annual and periodic spring-season fires. Thus the three experimental treatment units (approximately 25 ha each) per study area were designated as control (no fire), frequent burn, and infrequent burn. The frequent burn units were to be burned annually, 1996-1999. The infrequent burn units were to be burned twice, in 1996 and 1998 or 1999. After 1999, we plan to evaluate the initial effects, then continue burning with two distinct long-term treatments; fire applied every 2-3 years (frequent units) and fire applied every 5-6 years (infrequent units).

Fire treatment units were assigned nonrandomly to meet logistical needs. For WR and AR, populations of *Calamagrostis porteri* subsp. *insperata*, a state-endangered grass, were located in the central unit of each study area. To protect these populations from the unknown effects of fire, each central unit was designated a control (Figs. 5a and 5b). For YB and BR, the frequent and infrequent burn units were located adjacent to one another to facilitate burning as one large unit in years when both units are burned (Figs. 5c and 5d).

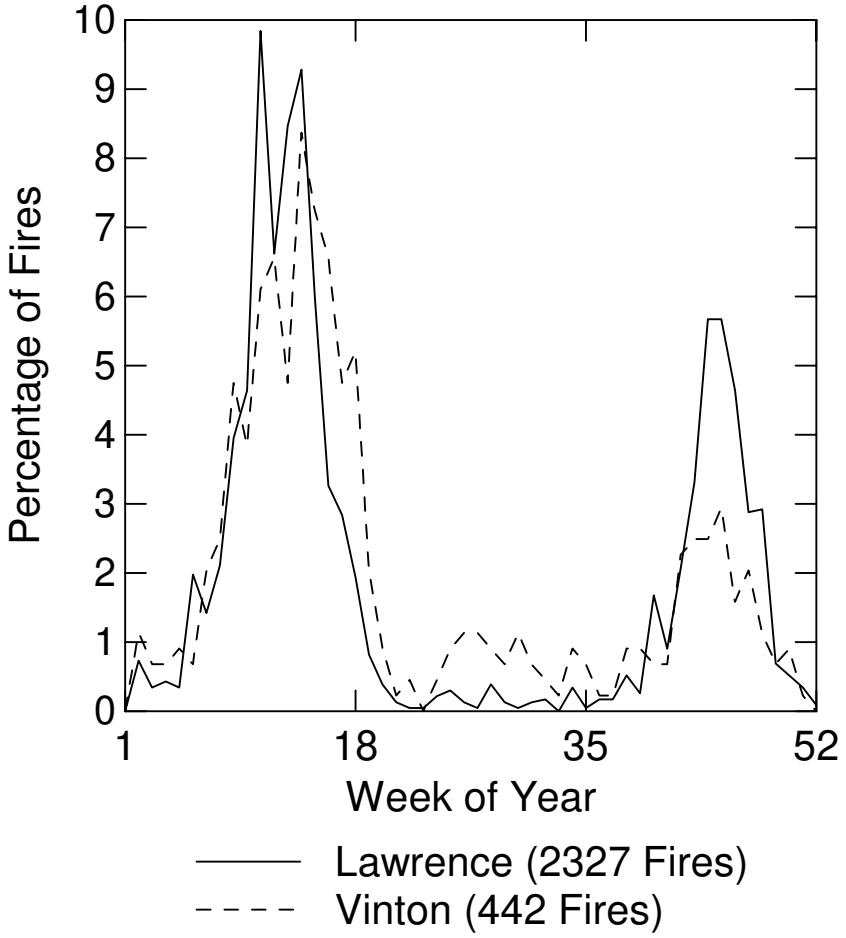

Figure 4.--Weekly percentage of total fires from October 1981 to October 2001 in Lawrence and Vinton Counties, Ohio.

Table 2.—Size of treatment units in each study area and the distribution of vegetation plots by IMI (integrated moisture index) class in each treatment unit.

Study Area	Treatment Unit	Area (ha)	Xeric plots	Intermediate plots	Mesic plots
Watch Rock	Control	20.4	3	2	4
	Infrequent burn	25.7	3	2	4
	Frequent burn	30.7	2	5	2
Arch Rock	Control	24.1	3	1	5
	Infrequent burn	24.0	3	3	3
	Frequent burn	32.0	4	2	3
Young's Branch	Control	24.1	3	3	3
	Infrequent burn	22.2	2	3	4
	Frequent burn	29.1	3	3	3
Bluegrass Ridge	Control	28.3	1	7	1
	Infrequent burn	49.8[1]	3	3	3
	Frequent burn	31.2	4	4	1
Total	Control	96.9	10	13	13
	Infrequent burn	123.0	11	11	14
	Frequent burn	121.6	13	14	9

[1]Includes an area of approximately 10 ha that was clearcut within the last 20 years and thus was not included in the study.

Soil Moisture (Integrated Moisture Index)

In the topographically dissected terrain of the region, aspect and slope position (rather than elevation) cause significant variability in microclimate, soil moisture, and nutrient cycling due to differential solar radiation and hillslope drainage patterns (Wolfe et al. 1949; Hutchins et al. 1976; Plymale et al. 1987; Garten et al. 1994). In turn, forest composition and productivity vary primarily along topographic gradients of moisture and fertility (Hutchins et al. 1976; Adams and Anderson 1980; Muller 1982; Fralish 1994).

To account for variation in soil moisture and vegetation, a geographic information system (GIS) was used in conjunction with forest-plot data to develop an Integrated Moisture Index (Chapter 3; Iverson et al. 1997). The integrated moisture index (IMI) was designed to integrate topography and soils into a single index that can be related to a number of ecological attributes across the landscape. The components of the IMI were a slope-aspect shading index (40 percent), cumulative flow of water downslope (30 percent), soil water-holding capacity (20 percent), and curvature of the landscape (10 percent). From the calculated IMI scores, 30 by 30-m cells were classified as xeric, intermediate, or mesic across the landscape (Figs. 5a-d). Chapter 3 provides a thorough description of the IMI and its application over the study areas.

Vegetation Sample Plots

We established vegetation plots within the treatment units to sample vegetation and soils. For each treatment unit, IMI maps were used to field-locate three 50 x 25 m (0.125 ha) vegetation plots in each of the IMI categories (Figs. 5a-d). Thus, there were three vegetation plots per IMI class, three IMI classes per treatment unit, and three treatment units per study area for a total of 27 plots per study area. During plot installation, slope corrections were made to locate plot corners, which were established permanently with reinforcement bar. Nearly all plots were located on sloping terrain; no plots were located in stream valleys or side-slope drainages and only a few plots were located on ridgetops. The plots were designed to sample trees >10 cm d.b.h. on the entire plot, tree saplings (1.4 m height to 9.9 cm d.b.h.) and seedlings (<1.4 m height) on one-half of the plot (25 x 25 m) and understory vegetation on the other half (25 x 25 m). Soil samples were collected adjacent to the vegetation plots (Chapter 5) and light measurements were taken at plot center (Chapter 6).

Established Design and Statistical Analysis

In summary, four study areas (Watch Rock, Arch Rock, Young's Branch, Bluegrass Ridge) were established as replicate blocks, each with three fire treatment units (control, infrequent burn, frequent burn) as whole plots. The whole plots were divided into subplots (split-plots) composed of three IMI classes (xeric, intermediate, mesic), resulting in 36 experimental units (four study areas X three fire treatments X three IMI classes). The three vegetation plots (sampling units) per IMI class in each treatment unit were designed as pseudoreplicates (Hurlbert 1984). When the established vegetation plots were georeferenced, 22 of 108 were located in an IMI class different from that intended. Thus, within each treatment unit, the number of vegetation plots per IMI class ranged from one to seven rather than three per IMI class (Table 2). However, 31 of the 36 experimental units contain two to five vegetation plots. Because all 36 experimental units contain at least one vegetation plot, the design is balanced at both the whole plot and subplot levels even though the number of pseudoreplicates is not balanced. Fauna sampling was not stratified by the IMI and was not linked to the vegetation plots; the experimental units were the 12 fire treatment units (Chapters 11 and 12).

For this volume, data collected on the vegetation plots were analyzed with a mixed-model analysis of variance (ANOVA) to determine whether there were significant pretreatment differences among fire treatments, among IMI classes, and fire*IMI interactions (PROC MIXED; SAS Institute 1999). Study area (block) was treated as a random effect, considered a random sample from a larger population of similar oak forests that can't be replicated exactly in other studies (Steel et al. 1997). Fire treatment and IMI class are treated as repeatable fixed effects. The statistical model assumes no interaction between block (study areas) and treatment (fire). The analyses presented in the chapters that follow will serve as a baseline to evaluate the subsequent effects of fire and IMI on many different ecosystem attributes.

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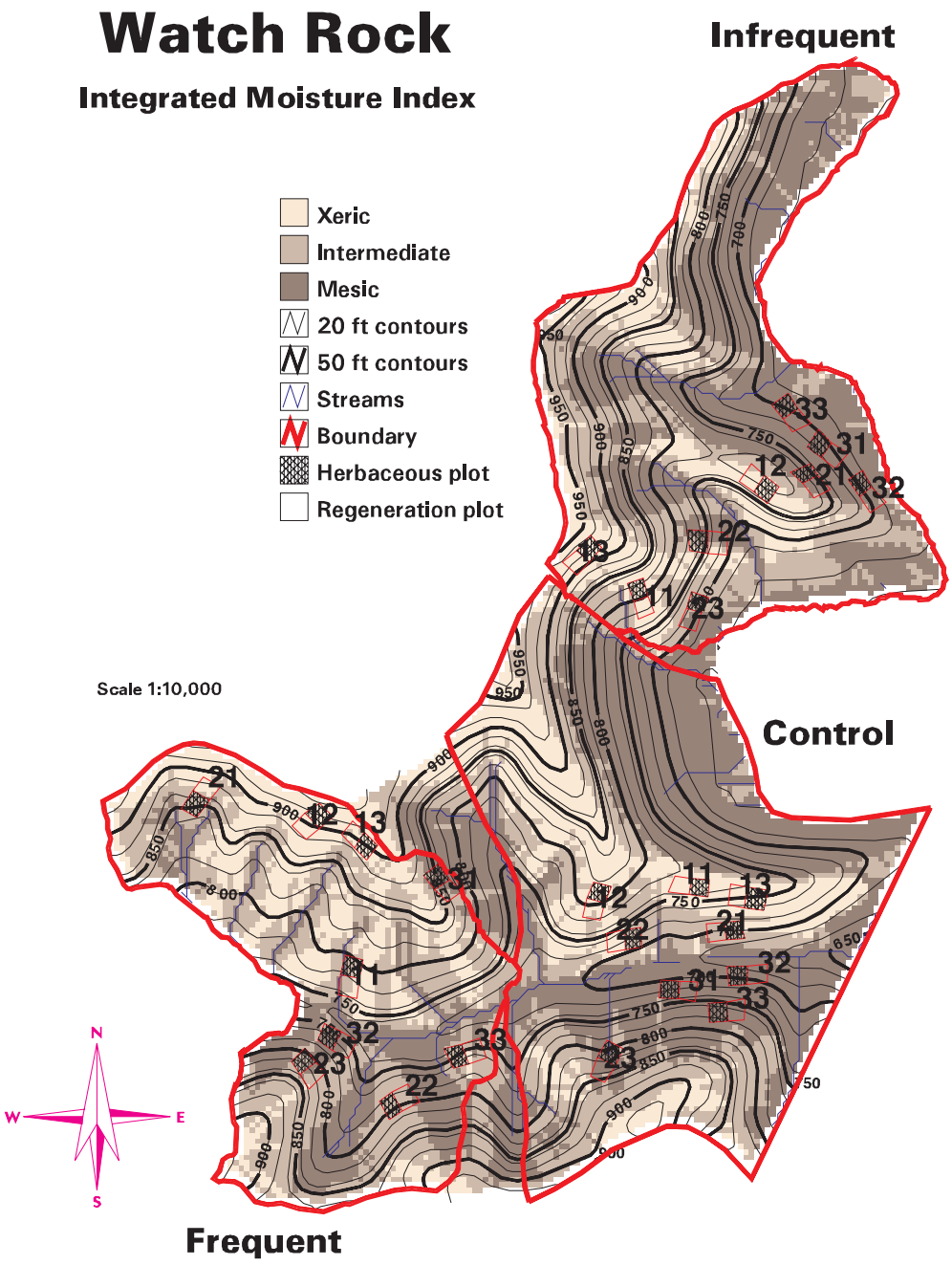

Figure 5a.-- Map of Watch Rock study area with fire treatment units, IMI classes, and vegetation plots. The total area comprises 76.8 ha.

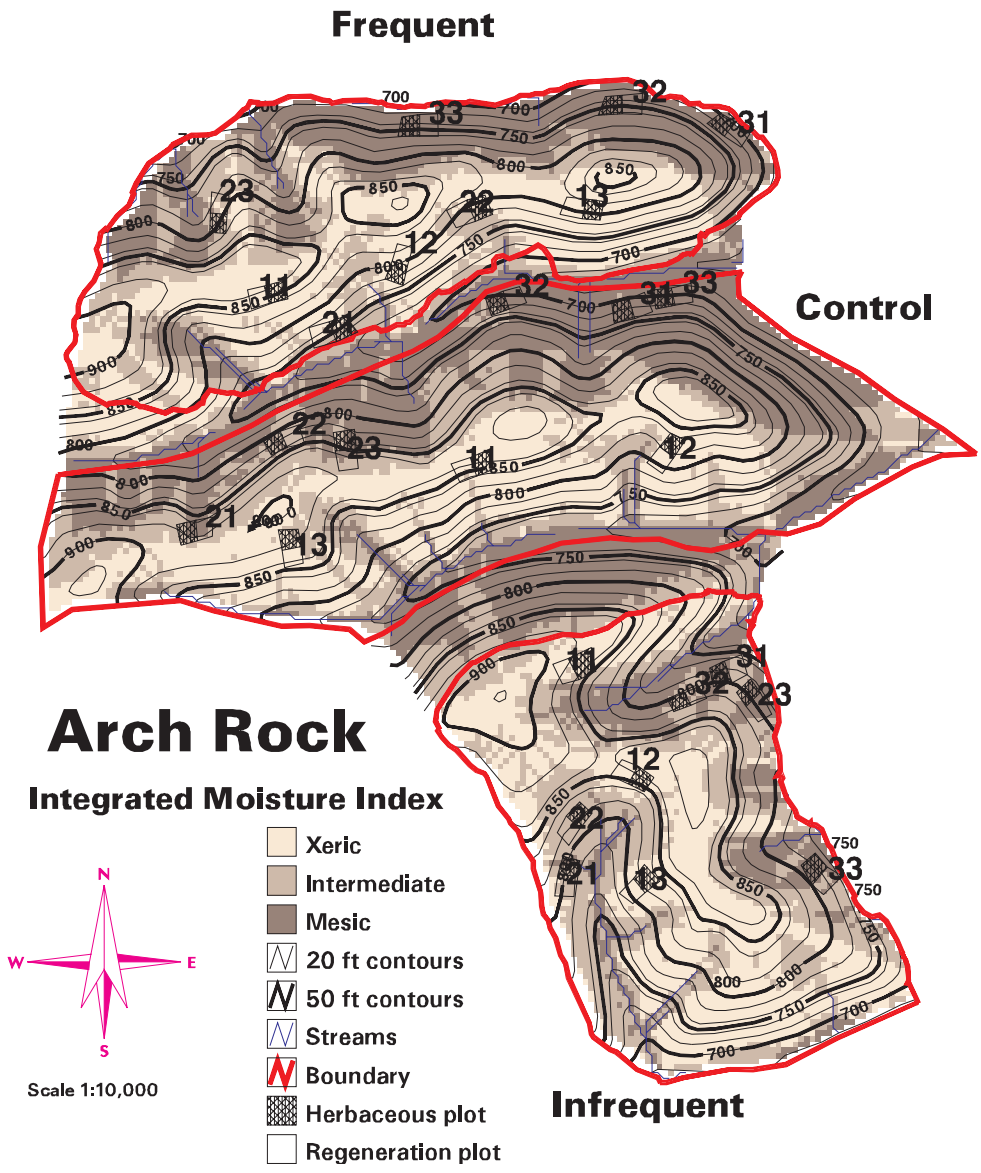

Figure 5b.-- Map of Arch Rock study area with fire treatment units, IMI classes, and vegetation plots. The total area comprises 80.1 ha.

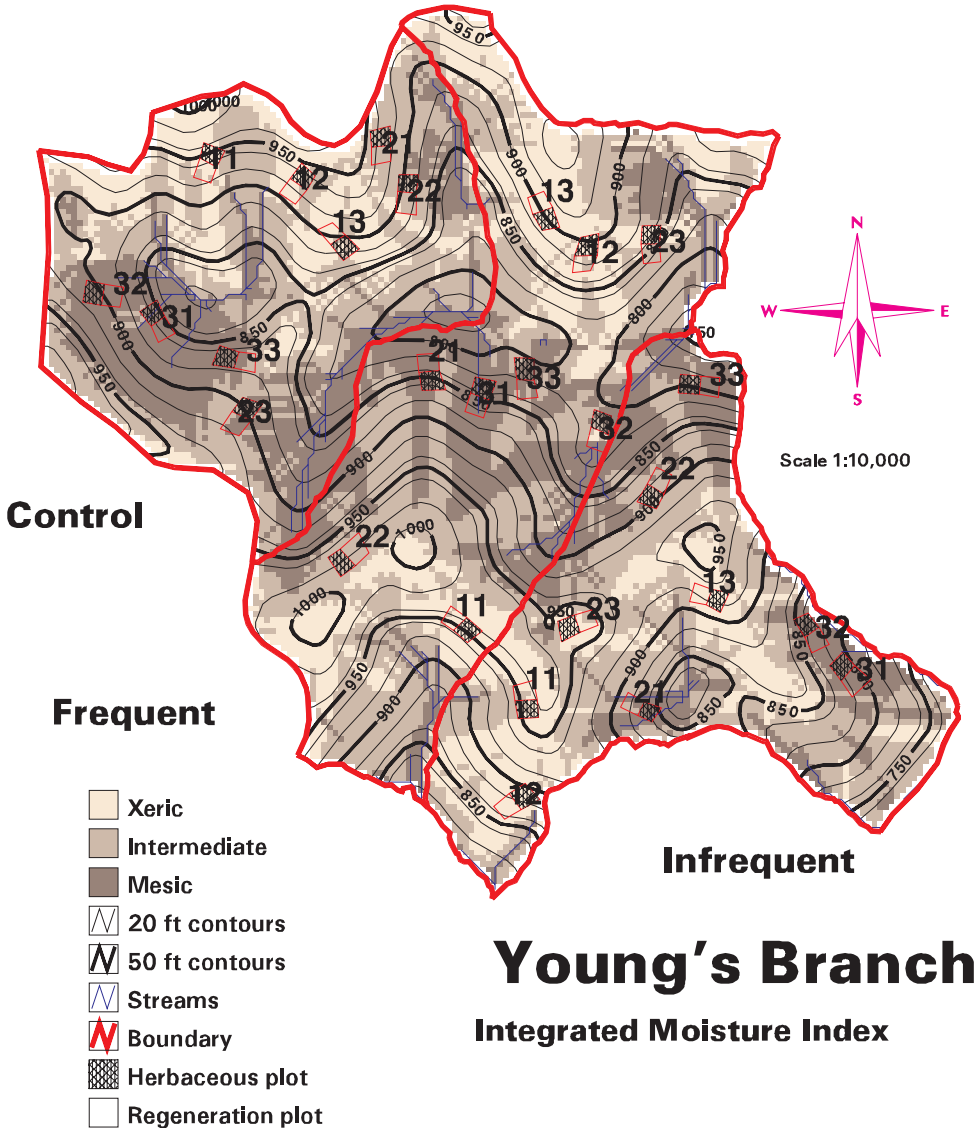

Figure 5c.-- Map of Young's Branch study area with fire treatment units, IMI classes, and vegetation plots. The total area comprises 75.3 ha.

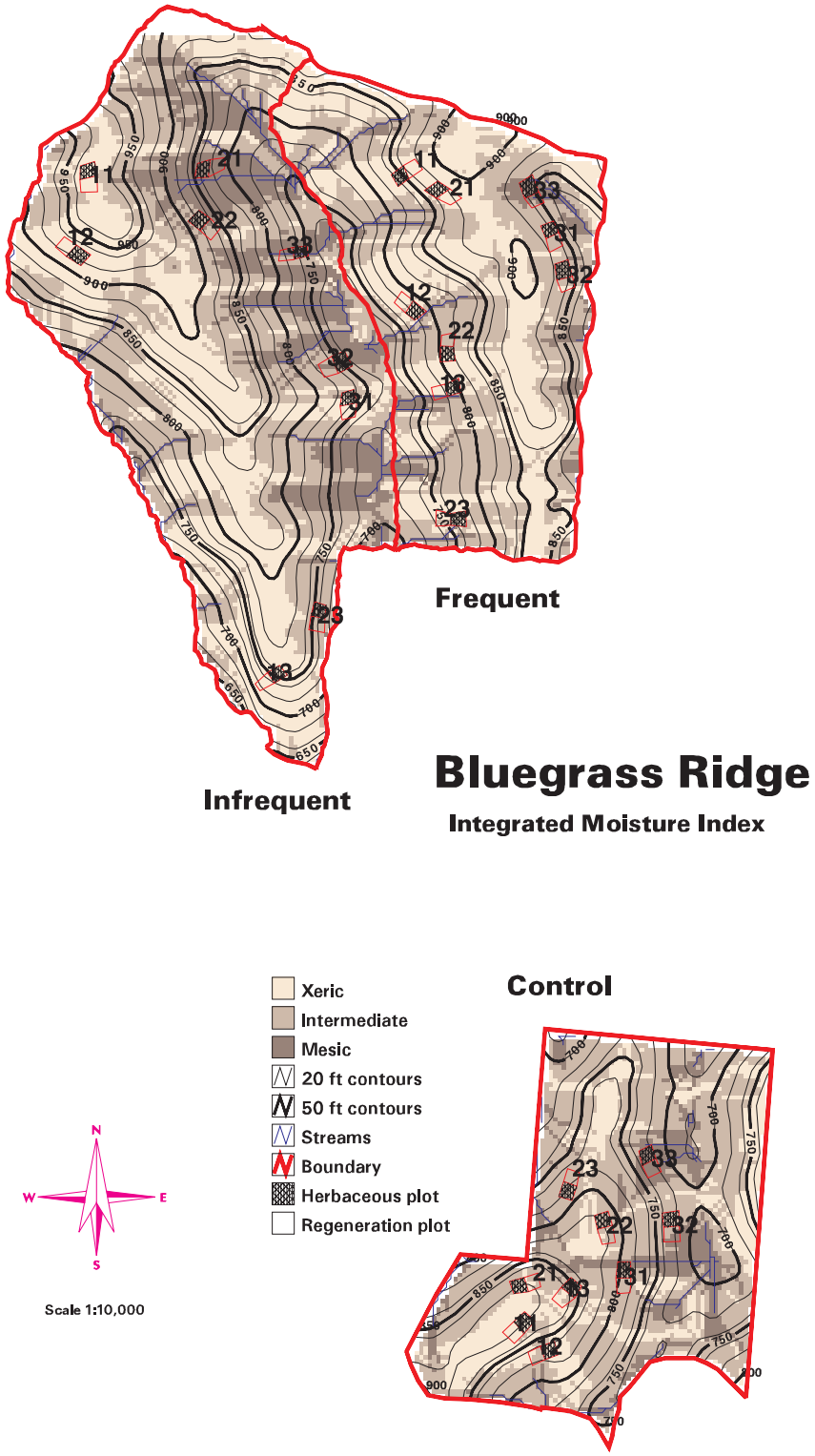

Figure 5d.-- Map of Bluegrass Ridge Study area with fire treatment units, IMI classes, and vegetation plots. In the infrequent burn unit, a recent clearcut (less than 20 years old) occupies approximately 10 ha of the unit in the west central portion. No vegetation plots are located in this area. The total area comprises 109.3 ha.

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Chapter 2

History of Forests and Land-use

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Abstract

Oaks (*Quercus*) have been a dominant component of eastern forests, including the forests of southeastern Ohio, for more than 5,000 years. Prior to Euro-American settlement, written accounts (1700s) described open, park-like forests and the use of fire by Native Americans for hunting and land management. In seven townships encompassing the four study areas, early land surveys (ca. 1800) indicate that 45 to 71 percent of the witness trees were oaks. White oak (*Quercus alba*) was the most common species; "black" oak (*Q. velutina* and *Q. coccinea*) and hickory (*Carya*) also were major components. Euro-American settlement of southeastern Ohio occurred in the early 1800s, but timber harvesting in the uplands was limited until the mid-1800s when the charcoal iron industry became prominent in the region. Iron furnaces were located near each study area, and the forests were clearcut for charcoal production until the industry declined in the 1880s and 1890s. These sites have since been undergoing secondary succession, though dendroecological analysis of release events in 119 white oak trees suggests some disturbance, likely from both anthropogenic (selective harvesting) and natural factors, since stand initiation in the mid- to late-1800s. Larger-scale releases have been more common at the Arch Rock and Watch Rock study areas. Oaks continue to dominate the overstory layer, but shade-tolerant species such as red maple (*Acer rubrum*), sugar maple (*A. saccharum*), blackgum (*Nyssa sylvatica*), and beech (*Fagus grandifolia*) now dominate the midstory and understory layers of all four study sites.

Introduction

To better understand the current characteristics of the mixed-oak forests in southern Ohio and to implement appropriate management strategies, it is important to know the land-use history and forest compositional trends of this region. Whitney (1994) noted that there are two primary sources of information available for historical ecology studies, written evidence (e.g., travelers' accounts, local histories, government documents) and field evidence (e.g., pollen analysis, disturbance history). In this chapter we use both written and field evidence to summarize the forest history of this region, with emphasis on land-use, disturbance, and forest composition of the landscape encompassing our four study areas since ca. 1800. The study areas are Arch Rock (AR) and Watch Rock (WR) in Vinton County, and Young's Branch (YB) and Bluegrass Ridge (BR) in Lawrence County. For a description of the study areas and experimental design, see Chapter 1.

Long-Term Forest Dynamics

Studies of pollen deposited in the sediments of bogs, ponds, and lakes provide a general view of broad-scale forest composition in Eastern North America over thousands of years (e.g., Delcourt and Delcourt 1987). Regional paleovegetation maps interpolated from numerous studies indicate that from 18,000 BP, the maximum advance of the Wisconsin glaciation, to 14,000 BP, southern Ohio was covered by boreal forest dominated by spruce (*Picea*) (Delcourt and Delcourt 1987). By 10,000 BP, the glacial front had retreated to southern Canada, and deciduous forests, with oaks (*Quercus*) as a major component, had replaced the northern mixed conifer-hardwood forest in most of Ohio (Webb 1981; Delcourt and Delcourt 1987). Oak pollen increased from 10,000 to 6,000 BP, and oak remained the dominant pollen type through 500 BP (Table 1).

Palynology studies have not been conducted near our study sites, but long-term pollen records have been documented within 250 km (Table 1). At Silver Lake, Ohio, oak pollen accounted for more than 40 percent of

Table 1. — Pollen percentages at several periods over the last 10,000 years in the general region of study areas.

Location	10,000 BP	6,000 BP	2,000 BP	500 BP
Silver Lake, OH[a]				
Oak	10-20	40-50	50-60	50-60
Hickory	<5	10-20	10-20	10-20
Maple	<5	<5	<5	<5
Cliff Palace Pond, KY[b]				
Oak	5-15	40-50	30-40	40-50
Chestnut	<5	<5	5-15	10-20
Pine	<5	<5	5-15	5-15
Maple	<5	<5	<5	<5
Regional interpolation for southern Ohio[c]				
Oak	20-40	40-60	40-60	40-60
Hickory	0-10	10-20	10-20	10-20
Maple	10-20	10-20	10-20	10-20

[a]Silver Lake located in Glacial Till Plains region, ca. 220 km northwest of Vinton County (data from Ogden 1966).
[b]Cliff Palace Pond located in Cumberland Plateau region, ca. 200 km southwest of Bluegrass Ridge (data from Delcourt et al. 1998).
[c]Data from Delcourt and Delcourt 1987.

the total pollen from 6000 to 500 BP; hickory also was a major component during that time. Maple (*Acer*) pollen accounted for less than 5 percent of total pollen throughout the pollen sequence. Similarly, oak pollen was the most abundant type at Cliff Palace Pond, Kentucky, for most of the period from 6000 to 500 BP, accounting for 30 to 50 percent of pollen. Hickory (*Carya*) was uncommon, but from 2000 to 500 BP, chestnut (*Castanea dentata*) and pine (*Pinus*) pollen were fairly abundant at the site. Maple pollen also occurred at less than 5 percent throughout the sequence at Cliff Palace Pond.

Native American Occupation and Land Use

Ohio was occupied by hunter-gatherers during the Paleo-Indian (ca. 17000 to 10500 BP) and Archaic (ca. 10500 to 3000 BP) Periods (Bush et al. 1995). More evidence of occupation exists for the Woodland Period (ca. 3000 to 400 BP), which is commonly divided into the Adena, Hopewell, and Late Woodland Phases.

Although southeastern Ohio was almost entirely forested at the onset of Euro-American settlement (ca. 1800; Gordon 1969), written accounts of the landscape prior to 1800 describe more open conditions in some areas. In 1751, Christopher Gist described the landscape approximately 60 km north of WR and AR study areas (near present-day Lancaster): "All the way from Licking Creek to this place is fine rich level land with large meadows, fine clover bottoms and spacious plains covered with wild rye" (Darlington 1893).

In several accounts, forests were described as open and park-like. In 1765, George Croghan frequently described "clear Woods" in eastern Ohio. Thaddeus Harris, traveling from Marietta, Ohio, to Wheeling, West Virginia, in 1802, wrote, "There is but little underwood; but on the sides of the creeks and near the river, the papaw, spicebush, or wild pimento and the dogberry grow in the greatest abundance" (Thwaites 1904).

Descriptions of open areas and park-like forests in the Eastern United States, in addition to direct accounts of Native Americans using fire, have led ecologists and historians to conclude that the use of fire as a land-management tool was widespread and had significant effects on the structure and composition of the landscape (Day 1953; Williams 1989; Whitney 1994). However, this conclusion is not universally accepted (e.g., Russell 1983), or may not be applicable to all forest types in the region (McCarthy et al. 2001).

Several accounts provide direct evidence of Native Americans using fire in the Ohio Valley. Joseph Barker ([1790] 1958), described burning near Marietta, Ohio

(85 km east of AR and WR study areas), "The Indians, by burning the Woods every Year, kept down the undergrowth and made good pasture for the deer and good hunting for himself." Traveling west from Pittsburgh, Pennsylvania, David McClure ([1772] 1899) noted that, "the woods were clear from underbrush, the oaks and black walnut do not grow very compact, and there is scarcely anything to incommode a traveler in riding, almost in any direction, in the woods of the Ohio. The Indians have been in the practice of burning over the ground, that they may have the advantage of seeing game at a distance among the trees." G. H. Loskiel, a missionary who lived among the Delaware and Iroquois in eastern Ohio and western Pennsylvania, described the use of fire during hunting (Loskiel 1794): "The Indians prefer hunting deer in large companies. Having surrounded a considerable tract of country, they let the dry leaves and grass on fire. The poor animals fly toward the middle to escape the flames, and the hunters closing in upon them, by following the fire, kill them with certainty, so that hardly one escapes."

Forest Composition from Early Land Surveys

Prior to significant settlement by Euro-Americans (ca. 1800), land surveys were conducted using the township and range system, and surveyors recorded the species and diameter of witness trees at section corners. Survey notes provide a unique quantitative record of forest composition and were used by Sears (1925) and Gordon (1969) to reconstruct the vegetation of Ohio just prior to Euro-American settlement.

In general, mixed-oak forests dominated much of the unglaciated Allegheny Plateau of southeastern Ohio (Gordon 1969). To develop a better understanding of the forests in the vicinity of our four study areas, witness-tree data were examined for townships encompassing and adjacent to the four sites. Summary data for three Vinton County townships adjacent to WR and AR were taken from Beatley (1959) and the original survey records for four townships adjacent to YB and BR were consulted; witness trees ranged from 7 to more than 100 cm in diameter at breast height (d.b.h.).

The most common witness tree in all seven townships was white oak (*Quercus alba*), which accounted for 32 to 45 percent of total witness trees per township (Table 2). "Black oaks," which probably included *Q. velutina* and Q. *coccinea* (Beatley 1959), and hickories (*Carya spp*.) also were major components. Less frequent upland species were chestnut oak (*Q. prinus*), American chestnut (*Castanea dentata*), and pine (*Pinus spp*.). Oaks accounted for 45 to 71 percent of all witness trees in the townships (Table 2).

Table 2. — Percentage of witness trees recorded in seven townships that included or were adjacent to the four study areas, recorded 1798-1805; for townships associated with AR and WR study areas (M/K = Madison and Knox, VI = Vinton, WI = Wilkesville), summary data are from Beatley (1959); for townships associated with YB and BR study areas (DE = Decatur, WA = Washington, AID = Aid, LA = Lawrence), original land survey notes were consulted.

		Arch Rock and Watch Rock			Young's Branch		Bluegrass Ridge	
Species	Survey name	M/K	VI	WI	DE	WA	AID	LA
Acer rubrum[a]	Maple	-	-	-	5	3	4	0
Acer saccharum	Sugartree	5	3	3	6	6	9	6
Carya spp.	Hickory	18	19	18	22	13	12	6
Castanea dentata	Chesnut	5	3	0	3	5	0	0
Fagus grandifolia	Beech	10	5	7	3	3	9	6
Liriodendron tulipifera	Poplar	4	1	2	3	3	3	3
Pinus spp.	Pine	0	0	0	1	0	2	2
Quercus alba	White oak	32	40	36	32	33	33	45
Quercus prinus	Chestnut oak	1	2	4	7	7	5	2
Quercus rubra	Red oak	0	0	0	1	0	1	0
Quercus velutina[b]	Black oak	12	18	18	3	3	12	24
Other tree species		13	9	12	15	25	11	4
Total trees[c]		196	163	115	180	120	152	161

[a]*Acer rubrum* may have been included with 'other tree species' or sugar maple in the AR and WR townships.
[b]Likely also included *Q. coccinea* (scarlet oak).
[c]Total number of witness trees used to calculate the percentages.

Species frequently recorded in the "bottoms" (stream valleys) but not abundant overall included beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow-poplar (*Liriodendron tulipifera*). Beech and poplar also were tallied in uplands, but sugar maple was confined primarily to the stream valleys. The surveyors recorded both "maple" and "sugartree," suggesting a distinction between red maple and sugar maple. "Maple," presumably red maple (*Acer rubrum*), was infrequent in the Lawrence County townships (zero to 5 percent of witness trees) and apparently was lumped into "other species" in the Vinton County townships (Beatley 1959).

In Washington and Lawrence townships, the surveyors also made brief mention of the "underbrush" in their line descriptions. Virtually every upland observation was of "oak and hickory underbrush" (presumably saplings and large seedlings); dogwood also was noted frequently. Spicebush (*Lindera benzoin*) was recorded in several stream valleys. Sapling species abundant in current forests, including red maple, sugar maple, blackgum (*Nyssa sylvatica*), and beech, were not recorded in the underbrush descriptions.

Euro-American Settlement

Euro-American settlement of Vinton County (WR and AR) began in 1805 (Willard 1916), and Aid Township (includes BR) was settled in 1815 (Bush et al. 1995). By 1850, 20 to 39 percent of forests had been cleared in Vinton County while less than 20 percent had been cleared in Lawrence County (Williams 1989). However, it is unknown whether forest clearing was significant in and around the study areas prior to the development of the charcoal iron industry. Unfortunately, we could not gather information on land use in our study areas for this period. Homesteading in the eastern United States generally consisted of creating a clearing in the forest for a house and crops (Williams 1989). Timber also was used for fencing and fuel while stock (both swine and cattle) was grazed in the surrounding forest (Williams 1989; Whitney 1994). In eastern Ohio, Howels (1895) described forest grazing in the mid-1800s: "In the summer our cows ran in the woods, which were unfenced, and the pigs... all they asked was a free range of the woods." In many wooded areas, fire was used to encourage the growth of grasses for livestock (Williams 1989).

Forest Clearcutting: The Charcoal Iron Industry

The charcoal iron industry (ca. 1830-1890) was the primary cause of the clearcutting of many forest stands in southeastern Ohio, including the landscapes containing the four study areas. In 1875 there were 69 iron furnaces in the Hanging Rock Iron District of southeastern Ohio and northeastern Kentucky (Stout 1933). The region had an abundance of iron ore deposits, limestone, and large tracts of old-growth timber for charcoal production (Stout 1933). The ore, usually less than 4 m beneath the surface, was mined and transported to the furnaces via ox carts. To supply charcoal for a typical furnace, 80 to 250 ha of forest were harvested annually, and secondary forests were harvested again at intervals of 20 to 30 years (Stout 1933). The timber was stacked into meilers, where it was slowly burned for 10 to 20 days to produce charcoal. Meiler locations have been noted in all four study areas (T. Hutchinson, pers. observ.).

Each study area is located within 2.5 km of at least one charcoal iron furnace (Table 3), and it is likely that each study area was clearcut when nearby furnaces operated. The iron industry began earlier and was more intense in the area surrounding YB (Table 3, Fig. 1). With the estimated cutting rotation of 20 to 25 years, the study areas probably were harvested more than once.

The discovery of richer iron ores near Lake Superior led to the decline of the charcoal iron industry in southern Ohio in the late 1800s (Morrow 1956). The depletion of the timber resource was also noted by Lord (1884): "It may be safely stated, that at present eight-ninths of this available timber land of the southern Ohio iron manufacturing districts has been cleared."

Land Use Since 1890

Following the decline of the charcoal iron industry, the study areas have been undergoing secondary succession. In 1991, Lawrence and Vinton were the most densely forested counties in the state with 77 and 79 percent forest land, respectively (Griffith et al. 1993).

Table 3.-- Charcoal iron furnaces located within 5km of the four study areas.

Study area	Furnace	Distance km	Date[a]
Watch Rock	Vinton	2.3	1853
Arch Rock	Eagle	3.1	1852
Young's Branch	Howard	1.8	1853
	Buckhorn	2.0	1833
	Mt. Vernon	4.1	1833
	Olive	4.4	1846
	Clinton	4.6	1832
	Bloom	4.8	1832
Bluegrass Ridge	Oak Ridge	1.0	1856

[a]Year that furnace began operating.

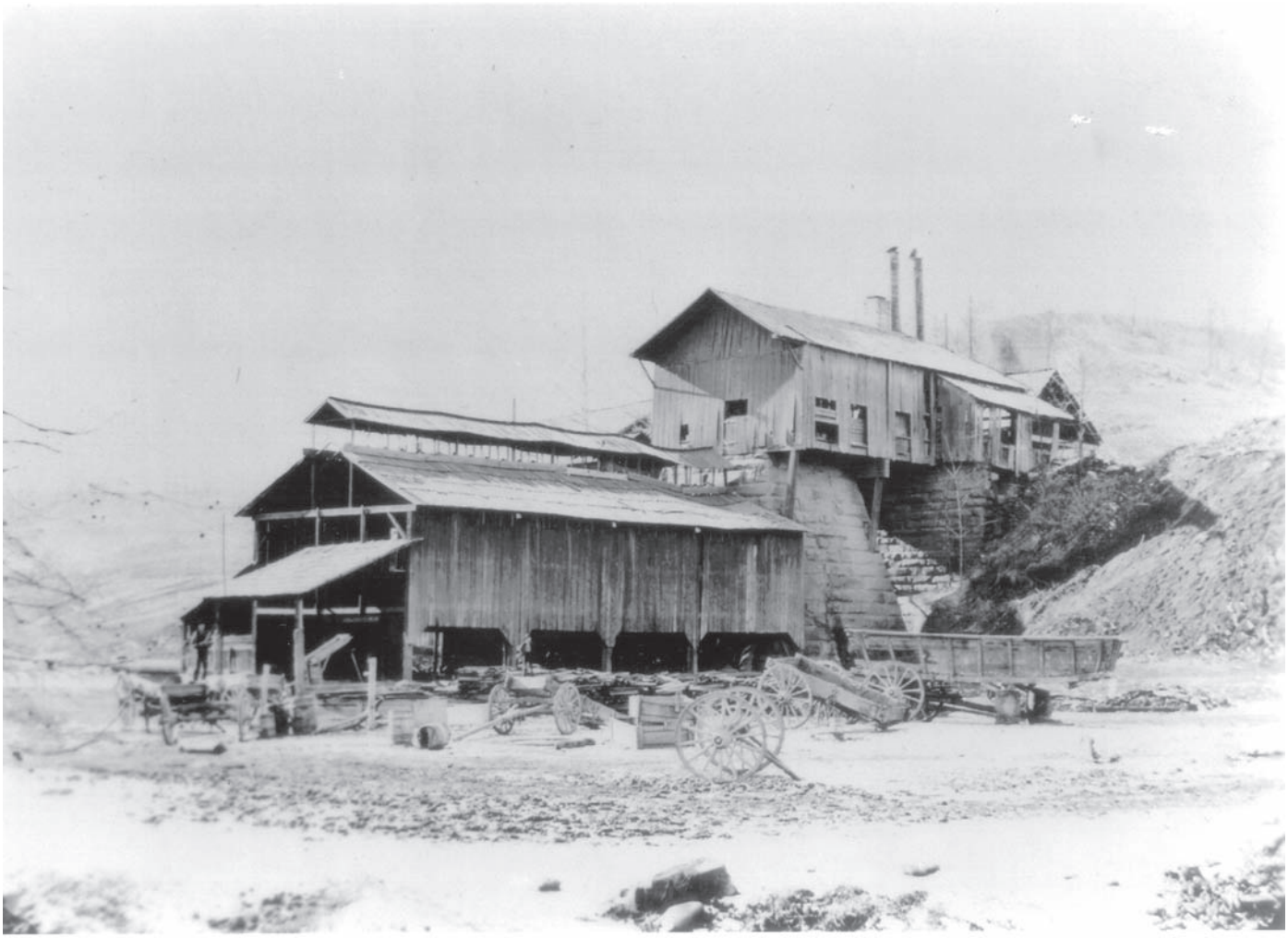

Figure 1.--The Buckhorn Iron Furnace (approximately 1875) was located 2 km from the current Young's Branch study area. Ox carts were used to transport rock containing iron ore and charcoal from the forests to the furnace. Note the cleared hillsides behind the furnace. (Ohio Historical Society photo).

Arch Rock and Watch Rock study areas

Vinton County plat maps indicate that the township sections that contain AR and WR study areas have never been subdivided into smaller parcels, which would indicate homesteading. There were small homesteads just west of AR until the 1930s; these were gradually abandoned during the Great Depression. Aerial photos from 1939 show a considerable amount of cleared land associated with the homesteads; however, the AR study area was closed-canopy forest. The families usually owned hogs or cows, which were grazed in the surrounding forest. Although there was no large-scale timbering during this time, the homesteaders did harvest some trees for cordwood, fencing, and railroad ties. Forests in the area were burned to improve visibility for detection of rattlesnakes and to increase blueberry (*Vaccinium*) production (Bill Pierce, pers. comm.) Aerial photos from 1939 show the area surrounding and including WR to be completely forested.

The D. B. Frampton Company owned much of the land that is now the Vinton Furnace Experimental Forest (within the Raccoon Ecological Management Area) from 1944 to 1962. The land was then acquired by Mead Paper Corp., the current owner (Kingsley and Dale 1985). The USDA Forest Service has conducted silvicultural research on these lands since 1952. There have been few fires and no grazing by domestic stock since the 1930s (Bill Pierce, pers. comm.).

Young's Branch study area

The YB units were acquired by the Forest Service in 1943. Nearly all of the land was closed-canopy forest in 1939 aerial photos, though the valley of Young's Branch (adjacent to the infrequent burn unit) was cleared and in agricultural use. Two of the mesic plots in the infrequent burn unit are only 65 to 70 years old, and some barbed-wire fencing is visible within the plots. Young's Branch is the only study area with evidence of iron ore mining. There are numerous ore pits (1 to 2 m deep), primarily on ridges and upper slopes, in all three units.

Bluegrass Ridge study area

The Forest Service acquired BR units FREQ (frequent burn) and INFR (infrequent burn) in 1936. The area had been divided into two major parcels prior to Forest Service ownership. Since the early 1940s, grazing by escaped livestock has been minimal and there have been no large fires (Ollie Bowling, pers. comm.). In the INFR unit, several of the intermediate and mesic plots are only about 65 years old.

The area encompassing the CONT (control) unit had been divided into three 40-acre parcels with different landowners prior to acquisition by the Forest Service; two parcels were acquired in 1965, one in 1992. Aerial photos from 1939 indicate that agricultural fields were present in the eastern drainage and hillsides adjacent to several of the vegetation plots. Tree cores indicated that these plots were relatively young, with the largest trees establishing between 1920 and 1925.

Dendroecological Analysis of Stand Histories

Tree rings offer a unique opportunity to assess the dynamics of individual stand conditions and disturbance regimes over relatively long periods, particularly when coupled with historical documents such as plat maps, travel journals, aerial photos, witness-tree records, and interviews (Lorimer 1985). The width of tree rings in a given year represents the radial-growth response of the trees to prevailing environmental conditions. Dendroecological analyses can determine how trees have responded historically to local stand conditions and stand dynamics (Fritts and Swetnam 1989).

To better understand the disturbance history of the four study sites, we performed a dendroecological analysis using 119 white oak trees (AR = 40, WR = 34, BR = 20, YB = 25). Tree cores were collected at a height of one meter using an increment borer. The cores were glued in grooved, wooden mounts and sanded with progressively finer grits of sandpaper for accurate dating and measurement (± 0.01 mm) of rings (Stokes and Smiley 1968). The dates and measurements were verified using COFECHA, a computer program that assists in scrutinizing date assignments and ring-width measurements (Holmes 1997).

For this study, we assume that stand disturbances can be discerned by identifying growth releases (i.e., sustained periods of high radial growth). Release events occur when favorable changes in the microenvironment (e.g., removal of a competitor) result in an increase of available resources (White and Pickett 1985). To describe the disturbance history of the study sites, we used a running median technique (an increase in radial growth of at least 25 percent when medians of adjacent 10-year growth segments are compared) to objectively identify release events. The criteria used in this method are adapted from Nowacki and Abrams (1997), who stated that 10-year growth increments are appropriate for the study of oak species growing in temperate, closed-canopy forests. Also, 10 years is longer than the duration of climatic events (e.g., prolonged drought) in the region, so sustained increases in radial growth should not be attributed to climate.

The approximate age for each stand was determined by calculating the mean age of the three oldest cored trees at each site; estimated stand initiation dates are shown in Figure 2. The exact year of stand initiation cannot be determined due to the presence of advance reproduction, missed inner rings (i.e., some increment cores were off-center and missed the pith), and trees were cored at one meter height (the time needed for a tree to reach one meter height is unknown). The current stands at all four study sites likely were initiated in the mid- to late-1800's. This period coincides with the period of decline in the charcoal iron industry in southern Ohio and subsequent land abandonment.

Comparison of the historical disturbance regimes of the four sites reveals several similarities but also differences in stand dynamics (Figs. 2-3). In the two Vinton County sites, AR and WR, many trees exhibit synchronous releases (at least 25 percent of the trees releasing in a given year) during the 1920s, 1940s, and 1960s-1970s. This synchronicity in release might be the result of several different disturbance agents. Given the regular periodicity (ca. 25 years), this disturbance probably is anthropogenic in origin and resulted from selective harvest or thinning. One can argue that the synchronous release during the 1940s might have resulted from the death of chestnuts during the 1930s. However, this scenario is unlikely because chestnut was not a major stand component (Braun 1950) and therefore, could not account for the high percentage of trees releasing (60 percent of AR and 42 percent of WR; Fig. 3). Further, a similar, synchronous release is absent at the YB and BR sites (Figs. 2-3). Finally, it is unlikely these synchronous release events are a natural stand development (e.g., self thinning) since the two sites differ in age (WR is about 20 years older than AR; Fig. 2).

One or more of these synchronous releases might have resulted from a major climatic event such as a severe windstorm or ice storm (i.e., glaze). However, we do not believe that the events were caused by wind because such a large area with different slope aspects and positions would have had to have been affected simultaneously. Also,

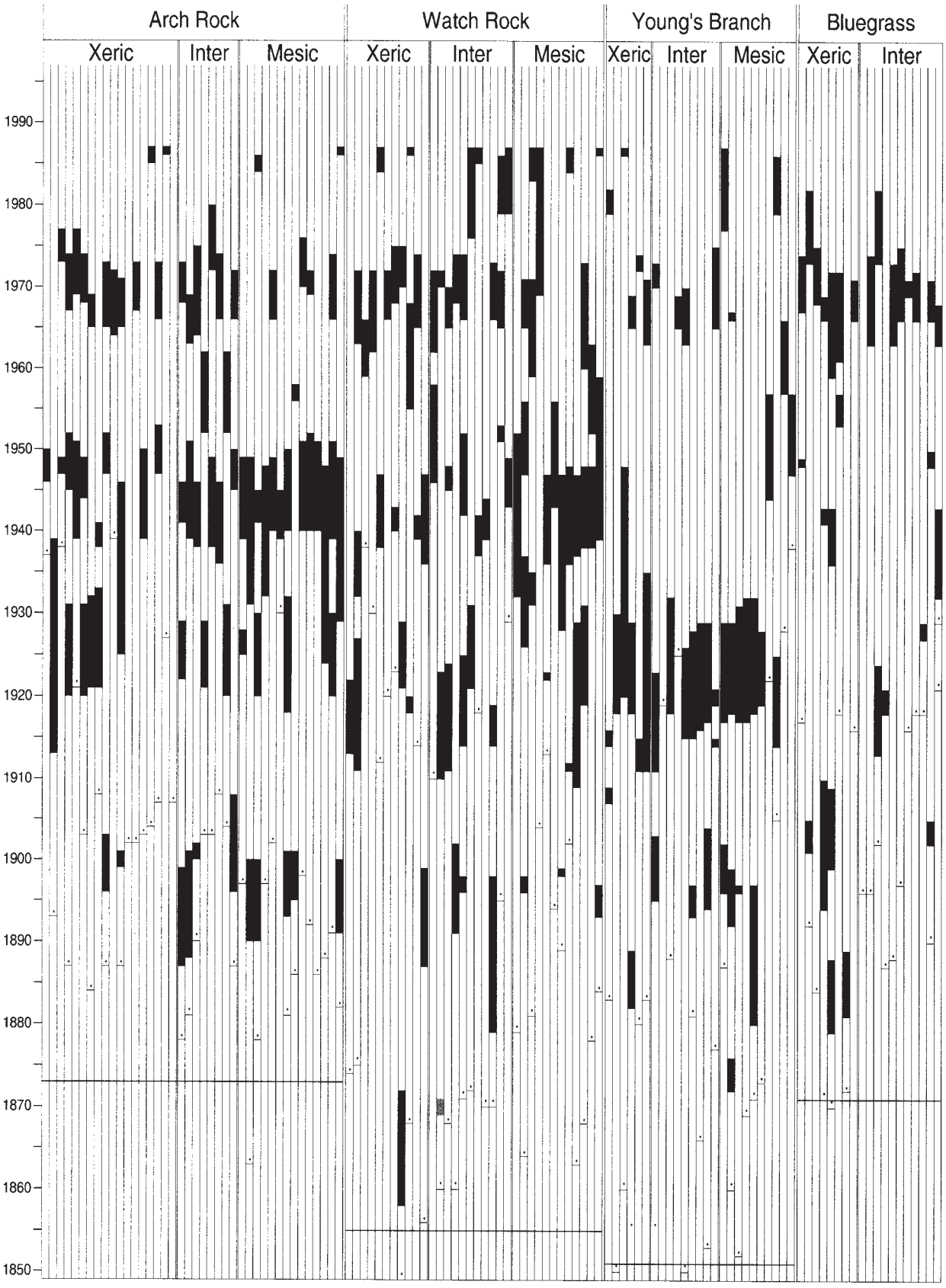

Figure 2.--Dendroecological recreation of historical disturbance events at the four study areas. Each column is a white oak and the shaded bars represent release events identified by the running median technique (see text). The first year of measured growth for each tree is indicated by the ⊥ symbol. The solid horizontal lines for reach study area represent approximate stand origination dates.

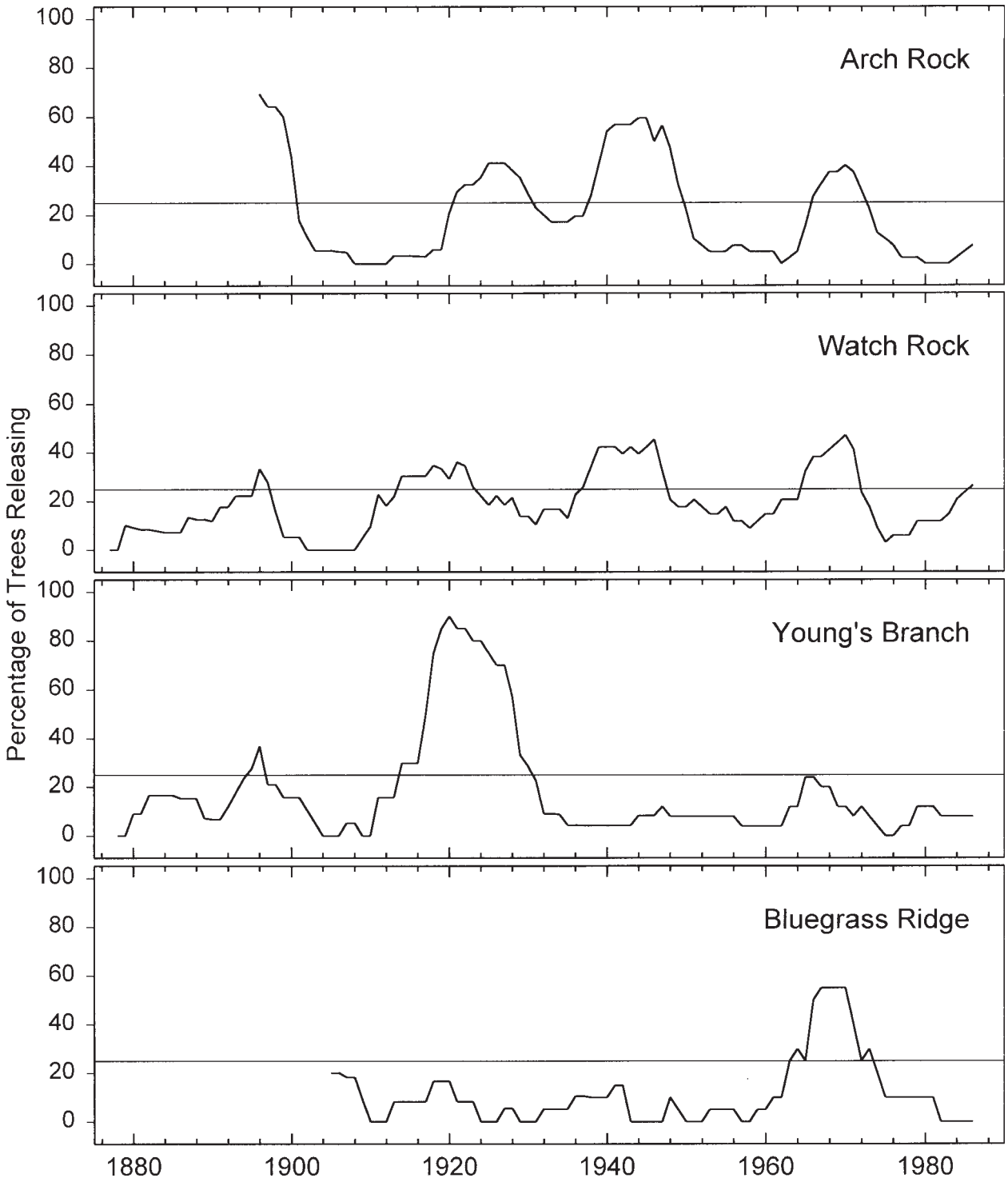

Figure 3.--Disturbance chronology of the four study sites. The percentage of trees releasing was determined by the running median technique. A synchronous release year is characterized by at least 25 percent of the trees releasing simultaneously.

strong winds and tornadoes are infrequent in southern Ohio, and the tornadoes that do occur in this region are likely not of a magnitude great enough to cause the widespread release patterns observed (Schmidlin 1996). Ice storms do represent a plausible explanation for the releases observed at the Vinton County sites. Ice storms affect trees differently according to canopy class, species, and topographic position (Bruederle and Stearns 1985; Mou and Warrillow 2000). Species such as white oak, which are considered moderate to low in susceptibility to ice damage, can survive ice storms and show accelerated growth following removal or damage of neighboring, susceptible trees (Boerner et al. 1988). Also, trees in the understory often are not as adversely affected as canopy trees and may fill storm-induced gaps and exhibit releases in radial-growth rate (Boerner et al. 1988).

At YB, many trees exhibit a simultaneous release from the 1910s through the 1930s; 90 percent of the cored trees released in 1920 (Fig. 3). Due to the magnitude of the release and the lack of a similar pattern at BR, the closest study site to YB, it is hypothesized that this massive release likely resulted from a silvicultural treatment.

All four study sites are characterized by a large number of trees exhibiting a release in the mid- to late-1960s through the 1970s. During the mid-1960s, drought was experienced in southern Ohio for several years. Of the 51 trees releasing during the postdrought period, 23, 20, and 8 were found in xeric, intermediate, and mesic Integrated Moisture Index (IMI) classes, respectively (Fig. 3). A chi-square test of homogeneity analysis revealed that the number of trees releasing in the various IMI classes was significantly different from an expected ratio of 1:1:1 ($\chi^2 = 7.41$; $P < 0.05$). Such results may be attributed to white oak's ability to tolerate drought conditions and regain normal growth following adverse conditions better than other species in more water-stressed microenvironments (xeric and intermediate sites). The AR study area contains stumps that may be the result of salvage logging in the area following the drought period or a coincidental silvicultural treatment.

Dendroecological analysis reveals both synchronous and asynchronous releases throughout the four study sites (Figs. 2-3). Such patterns suggest that both anthropogenic and natural processes (gap-phase dynamics or large-scale climatic events; Runkle 1985) likely influenced stand structure and dynamics here.

Current forest trends

Shade-tolerant tree species (e.g., red maple, sugar maple, blackgum, and beech) now dominate the sapling layer (see Chapter 8) and the smaller size classes (10 to 20 cm d.b.h.) of the tree layer (Chapter 9) in all four study areas. Similar shifts in species composition have been documented in oak forests throughout the Eastern United States. Although numerous factors have been implicated in the widespread decline of oak regeneration, suppression of fire since the 1940s is hypothesized to be a primary cause (e.g., Lorimer 1984; Abrams 1992).

Acknowledgments

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Chapter 3

A GIS-Derived Integrated Moisture Index

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Abstract

A geographic information system (GIS) approach was used in conjunction with forest-plot data to develop an integrated moisture index (IMI) that is being used to stratify and help explain landscape-level phenomena in the four study areas. Several landscape features (a slope-aspect shading index, cumulative flow of water downslope, curvature of the landscape, and water-holding capacity of the soil) were used to create the IMI in the GIS. The IMI can be used to better manage forest resources where moisture is limiting and to predict how the resource will change under different forms of ecosystem management. In this study, the IMI was used to stratify the study areas into three moisture regimes: xeric, intermediate, and mesic. Of the 108 plots established across the four study areas (27 per study area), roughly a third fell into each of the three moisture classes. The proportion of land in each IMI class was similar among study areas. The Watch Rock site had the highest proportion area in the mesic class, while Bluegrass Ridge had the highest proportion of land in the xeric class. Among treatment areas within each study area, the distribution of IMI classes was similar, so that treatment effects can be attributed to the treatments rather than a priori landscape variation. Analysis of IMI by vegetation plot revealed that these plots well represent the entire treatment areas.

Introduction

Trends in Forest Composition in Ohio

Ohio is typical among many Midwestern and Eastern States in that oaks, e.g., white (*Quercus alba*), chestnut (*Q. prinus*), scarlet (*Q. coccinea*), black (*Q. velutina*), and northern red (*Q. rubra*), are being replaced by maples (*Acer rubrum* and *A. saccharum*) and other species in historically oak-dominated forests. Data from USDA Forest Service inventories between 1968 and 1991 (Kingsley and Mayer 1970; Dennis and Birch 1981; Griffith et al. 1993) indicate that the proportion of total overall volume in oak and hickory *(Carya* spp.) declined substantially compared to maple, black cherry (*Prunus serotina*), and yellow-poplar (*Liriodendron tulipifera*) (Fig. 1). Although absolute growing-stock volumes tended to increase for most species in Ohio as the secondary forests matured, there was a shift in the relative importance of species: red oaks declined by 41 percent relative to total volume, while white oaks and hickories showed a relative decline of 31 and 22 percent, respectively. By contrast, relative increases (as a proportion of total volume) were documented for red maple (70 percent), sugar maple (44), black cherry (129), and yellow-poplar (38). This trend corroborates a pattern seen regionwide, e.g., in Illinois (Iverson et al. 1989; Iverson 1994), Pennsylvania (Abrams and Nowacki 1992), and several other Eastern States (Powell et al. 1993). This trend has prompted a large scientific effort to assess the problem and search for management solutions (e.g., Loftis and McGee 1993). In southern Ohio, a large-scale ecosystem management project was established in four study areas to study the effectiveness of using prescribed fire for oak ecosystem restoration. In this chapter we describe the development and application of an Integrated Moisture Index (IMI) across the study sites.

Tree Species Regeneration Related to Environmental Factors

It has been shown that the success of oak regeneration is related to light and moisture gradients. Oaks do not regenerate well under moist, shady conditions in the absence of fire, and thus are declining in importance across the Eastern United States while more shade-tolerant, mesophytic species are gaining (Heiligmann et al. 1985; Hilt 1985; Loftis and McGee 1993; Barton and Gleeson 1996). Oaks generally are classed as intermediate in tolerance to shade. Compared to tolerant species such as red maple, oaks have a higher light compensation

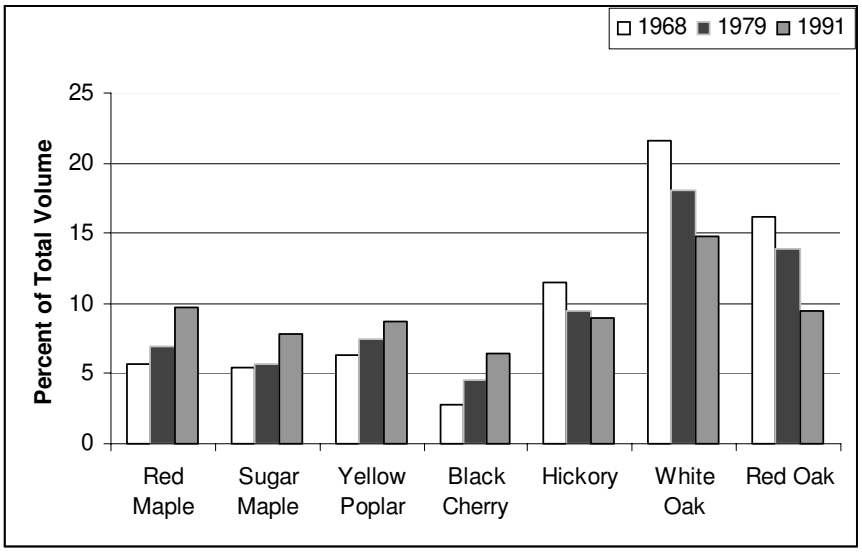

Figure 1.—Forest-inventory trends for seven primary species or species groups in Ohio, 1968-91 (Source: Kingsley and Mayer 1970; Dennis and Birch 1981; Griffith et al. 1993).

point, use light flecks less efficiently, have similar or lower rates of net photosynthesis, higher rates of respiration, and lower biomass yields (Hodges and Gardiner 1993). Yet oak also is at a disadvantage when light is not limiting (e.g., following a clearcut); in this case, yellow-poplar and other intolerant species tend to grow faster and outcompete the oaks (Beck 1990; Marquis 1990). Net photosynthesis is significantly greater in intolerant species than in oak; photosynthesis in oak saturates at one-third of full sunlight, much less than that for intolerant species (Beck 1990; Marquis 1990). Intolerants also allocate a greater portion of photosynthate to shoot growth, giving them a height advantage over oaks (Hodges and Gardiner 1993).

Oaks are relatively more tolerant of moisture stress due to morphological and anatomical characteristics of oak leaves and xylem and patterns of carbon allocation that favor root growth. These factors enhance growth and give oaks a competitive advantage under moisture-stressed conditions (Hodges and Gardiner 1993).

Thus, conditions for oak regeneration are best where light levels are intermediate and where long-term soil moisture levels are limited (Loftis and McGee 1993). For much of the mixed-oak region of the United States, future oak-dominated natural stands likely will be concentrated in relatively dry landscape positions where competition from more mesic and shade-tolerant species will be minimized. If a high level of oak in the stand is a desired condition, management activities should be concentrated in areas with intermediate to mesic moisture levels, i.e., where oak regeneration is low, but where fire and/or silvicultural practices such as group selection cuts could shift the balance in favor of oaks.

If current trends continue, red maple likely will be the dominant future canopy tree over much of the mixed-oak forest type as it grows on a wider range of soil types, textures, moisture, pH, and elevation than other forest species in North America (Hepting 1971; Golet et al. 1993; Iverson et al. 1999). It is expanding in dominance throughout its range (Abrams 1998) and can thrive following many kinds of disturbance (Bowersox and Ward 1972; Good and Good 1972). However, red maple is highly susceptible to fire because of its thin bark (Hengst and Dawson 1994).

Several other ecosystem properties are correlated to moisture gradients. Nitrogen availability and pH both tend to be higher with higher moisture regimes (Hairston and Grigal 1994; Garten et al. 1994; Morris and Boerner 1998), and long-term soil moisture has been used to predict organic matter, phosphorus, and depth of the A horizon (Gessler et al. 1995). Plant composition also is strongly related to these gradients, including overall biological diversity which tends to be greater under higher moisture regimes (Host et al 1987; Iverson et al. 1999; Hutchinson et al. 1999). These gradients are increasingly being related to animal distributions as well. For example, Dettmers and Bart (1999) used moisture regimes derived from landscape parameters to predict suitable habitat for several species of birds in Ohio.

Moisture Models and Tree Growth

The distribution and growth (i.e., site index) of trees in this geographic region are correlated with local topography and soils, but these relationships are difficult to quantify and map (Merz 1953; Trimble and Weitzman 1956; Trimble 1964; Carmean 1965; Tajchman and Boyles 1993). McNab (1993) devised a topographic index based on eight slope gradients that was related to yellow-poplar site index in the southern Appalachians. Fralish (1994) found a strong relationship between stand basal area and soil and topographic factors in southern Illinois. He found this association related mostly to the soil-water reservoir. Slope angle, aspect, and position, and effective soil depth were the primary factors controlling the

amount of water in the soil-water reservoir. White (1958) also concluded that any measure of site productivity is mostly an estimate of the amount of available soil water, the exception being when the site has a prevailing water table within 2 m of the surface where ground water would be available for tree growth (Loucks 1962). In British Columbia, Wang and Klinka (1991) found that the site index for lodgepole pine (*Pinus contorta*) could be estimated reasonably well with a soil-moisture model. Host et al. (1987) reported that forest successional pathways in Michigan were strongly related to topographic and edaphic conditions, again, largely via variations in moisture availability.

These relationships indicate that geographic information system (GIS) technology may be ideally suited to model moisture level across landscapes, and, by extension, the ecosystem patterns and processes correlated to moisture, including oak regeneration. Predictive vegetation mapping has advanced rapidly in recent years because of the increased availability of digital maps of topography and soils, and tools for processing them (Franklin 1995). Digital elevation models (DEM) (U.S. Geol. Surv. 1987) have been useful in deriving topographic features associated with landscape processes (Jenson and Domingue 1988; Skidmore 1990; Twery et al. 1991; Garten et al. 1994; Mitasova et al. 1996). Digital elevation data also have been used in combination with remotely sensed and other data to map forest composition and biomass (Fox et al. 1985; Frank and Thorne 1985; Iverson et al. 1994).

The objectives of this study were to: 1) create a model predicting an integrated moisture index (IMI) based on DEM and soils data; 2) apply the model across the study areas of the ecosystem management project to stratify the landscape into moisture classes; and 3) summarize IMI and other landscape features prior to prescribed fire treatments.

Methods

Integrated Moisture Index

The IMI was developed to integrate GIS-derived topographic and soil features of the landscape into a single index that can be statistically related to a number of ecological processes across a landscape (Iverson et al. 1996; Iverson et al. 1997). The intention was to provide a relative rating of moisture that can be related to specific processes wherever moisture is seen as the primary driving factor. Assuming reasonably similar climate, elevation, disturbance history, and soil fertility among upland sites, variation in plant distribution and productivity is driven primarily by moisture availability. Moisture levels are higher where direct solar radiation is minimized (the hillshade variable in the IMI model), in lower positions on slopes (flow accumulation) or in depressions (curvature), and in soils capable of storing large amounts of water (total water-holding capacity). Therefore, IMI is modeled here as a function of:

solar radiation potential, or hillshade +
flow accumulation of water downslope +
curvature of the landscape +
total available water capacity of soil

The first three factors (hillshade, flow accumulation, and curvature) were generated from U.S. Geological Survey (USGS) 7.5-minute DEM data (1:24,000 scale, 30x30 m cell size). This method is described in detail in Iverson et al. (1997).

Hillshade captures the effects of differential solar radiation due to variation in slope angle, aspect, and position, and accounts for shading from adjacent hills. The latter component of hillshade was minimal because, although dissected heavily, the maximum relief change was less than 100 m and cliffs are rare in the area. Cumulative solar radiation is greatest on steep, south-facing slopes (Lee and Baumgartner 1966). Because of the added drying potential of higher afternoon temperatures, drying of soil is greatest on aspects slightly west of south (SSW). Thus, the highest moisture levels will be on NNE aspects, a solar azimuth of 22 degrees. A solar altitude of 45 degrees was used to approximate a growing season average. The "hillshade" command in Arc/Info Grid (Environ. Syst. Res. Inst. 1994), operating on the digital elevation data for the sites, was used to create hillshade maps with increasing scores contributing to increasing moisture content.

Flow accumulation represents the accumulated flow of water downslope as water moves via gravity. Thus, it is related to position on the slope where the bottoms of slopes accumulate much more moisture than ridgetops. The Arc/Info Grid command "flow accumulation" (Environ. Syst. Res. Inst. 1994) counts the number of cells sending water downslope to the cell being evaluated; ridgetops would have a flow accumulation of only one while the valley bottoms would have maximum accumulation. Thus, higher flow accumulation scores contribute to higher IMI values.

Curvature is a measure of shape of the topography. The Arc/Info program "curvature" assesses surrounding cells to calculate a curvature, with increasing positive scores representing increasing concavity. Concave surfaces will accumulate moisture and contribute positively to the IMI. The curvature map generally assigns small coves and depressions with higher scores, and small knolls with lower scores. Algorithms for flow accumulation and curvature are given in Jenson and Domingue (1988).

Total available water capacity was derived from digitized soil-series maps originally compiled at a scale of 1:15,840 by the USDA Natural Resources Conservation Service. Using the attributes from these soil maps, soil depth (A plus B horizons) and available water capacity (per unit depth) were multiplied to estimate the total amount of water available to plants in the A and B horizons. In several instances, the mapping unit was a soil complex consisting of two or more soil series; in these cases, weighted averages were calculated based on the percentage of each soil series in the complex. There was a large difference in total water-holding capacity between bottomland and upland soils. The latter are mostly shallow soils with bedrock close to the surface, which severely restricted the total water-holding capacity. Soils in the valleys generally were deeper with higher silt content. These maps generated for total available water capacity had sharp boundaries with large differences in water capacity depending on the mapped soil series/ complex. A continuous soil-property map developed using GIS and fuzzy logic would be preferable, and is being developed by some researchers (e.g., Zhu 1994; Ramlal and Beard 1996).

Each of the four factors cited were standardized to a score of 0 to 100 to facilitate calculation of the IMI. After numerous iterations associated with on-site visits and field experience, the weights selected for use in the GIS model for the IMI were hillshade (40 percent), flow accumulation (30), total water-holding capacity (20), and curvature (10). The final IMI score has a theoretical range of zero to 100, with higher scores indicating higher soil moisture levels.

Stratification of Study Sites

The resulting IMI scores, along with minimum size requirements were used to stratify the sites into four classes:

1. **xeric**: IMI scores 0-35.0
2. **intermediate**: 35.0-50.6
3. **mesic**: 50.6-100
4. **too small**: < 4000 m^2

Obviously, these class breaks are artificial and were selected in order to achieve good representation of each class. These classes were mapped and used in the field to position the vegetation and soil plots into the approximate moisture regime. Later, when a global positioning system (GPS) became available to us, precise calculation of IMI and IMI class was performed for plots.

Map Generation and Georeferencing

Maps were generated for each site and IMI classes were mapped as described. Topographic lines were generated from the DEM via an ARC/INFO GRID program (Contour) (Environ. Syst. Res. Inst. 1994).

GPS technology was used to georeference unit boundaries and plot locations (108 plots across the four study areas, three treatment units, three IMI classes, and three replicates) (see Chapter 1). A Trimble ProXL GPS was used to acquire the line data for the firelines for the fire-treatment units. The data were then differentially corrected with Pathfinder software (Trimble Navigation Ltd. 1995) and imported into Arc/Info, where the data were edited to remove spurious vertices, and built into polygon coverages. Because the control treatment unit boundary lines were generated via digitization of lines drawn on 1:24,000 scale topographic maps, these data are therefore not as accurate as the GPS data.

As discussed in Chapter 1, the individual plots measure 25 x 50 m and are bounded by six metal stakes. Each stake was positioned with 150 GPS points and later was differentially corrected to within ~3 m with the Pathfinder software. The points were transferred to the GIS and converted to plot-boundary polygons for GIS mapping and analysis. Understory vegetation and regeneration subplots were identified separately in the GIS for later analysis.

Analysis by Study Site

The GPS and GIS efforts allowed calculation of area and proportions of each IMI class for each study area: Arch Rock (AR), Watch Rock (WR), Young's Branch (YB), and Bluegrass Ridge (BR). This analysis resulted in overall statistics on area and perimeter of each treatment area in each study area, along with average IMI scores and percentages in each IMI class.

Analysis by Treatment Area

The GIS was used to assess the following characteristics for each treatment unit: area, average IMI, hillshade, flow accumulation, curvature and soil water-holding-capacity scores, average slope angle, average, minimum, maximum and range of elevation, and length of streams and ridges within the treatment units. Site index for oak also was estimated based on regression relations developed earlier between IMI and young forest stands near the Vinton County sites (AR and WR) (Iverson et al. 1997). These characteristics were used to assess landscape variability within and between study areas.

Analysis by Plot

Each of 108 plots was located accurately in the GIS via GPS. The plots were subsampled to 2-m pixel cells and overlaid via Arc/Info Grid on a series of map layers to

generate weighted-average statistics for each plot. Thus, statistics were generated for the following landscape characteristics: IMI, hillshade, flow accumulation, soil water-holding capacity, curvature, aspect in degrees, slope angle, elevation, distance to nearest stream and to nearest ridge, and estimated oak site index. The aspect in degrees was simply an average aspect in degrees, with proper accounting when pixels within a plot had a mixture of aspects east (< ˉ45º) or west (> 315º) of due north.

Results and Discussion

IMI Generation

The resulting models of IMI for the four study areas reveal the heterogeneous nature of the landscape. For example, within any 10-ha area, one can find a wide range of IMI scores (Fig. 5, Chapter 1). There is also a general pattern of low scores (drier conditions) on ridgetops and south-southwest facing slopes, especially where soils are shallow. The deep soils and high flow accumulation along stream bottoms such as the Elk Fork (the eastern boundary of AR FREQ (frequent burn unit) and WR INFR (infrequent burn unit) are apparent with the highest IMI scores.

Descriptive Statistics by Study Area, Treatment Area, and IMI Category

The average IMI score, and the proportions of each treatment or study area within the three IMI classes were reasonably consistent across study areas (Table 1). These sites encompassed 341.5 ha, 244.6 of which were FREQ or INFR treatment areas. Except for the 49.8-ha INFR treatment area on BR, all treatment units range in size from 20.4 to 32 ha. Weighted-average IMI scores by treatment unit ranged from 39.2 on AR INFR to 50.1 on WR CONT (Table 1). WR was the most mesic with 41 percent of its area in that class, while BR was the least mesic with only 15 percent of its land being in that class (Table 1). AR and YB had 29 and 31 percent of the area classified as mesic, respectively. An underlying reason for the smaller proportion of mesic land at BR was that its ridgelines generally run north to south, while the other sites have generally east to west ridgelines. North-south ridges result in less north-facing terrain; hence, IMI values are lower. This trend also was apparent for the AR INFR treatment area, with only 18 percent mesic land (Table 1).

Landscape features, including the variables used in creating IMI, also were calculated for each IMI class within the treatments and study areas (Table 2). For three of the four components of IMI (except for several instances of water-

Table 1.—Summary information by study and treatment area.

Study Area	Treatment	Area	Perimeter	Average IMI	Xeric	Inter-mediate	Mesic
		ha	*m*		*Percent*		
Arch Rock	Control (B)	24.1	2451	46.3	32	31	37
	Frequent (A)	32.0	2898	44.2	39	29	33
	Infrequent (C)	24.0	2123	39.2	43	39	18
	Total/Average	80.1	7472	43.3	38	33	29
Watch Rock	Control (B)	20.4	2223	50.1	23	28	49
	Frequent (A)	30.7	2592	42.3	31	45	25
	Infrequent (C)	25.7	2650	49.4	19	32	49
	Total/Average	76.8	7465	46.7	24	35	41
Young's Branch	Control (A)	24.1	2340	45.2	21	44	35
	Frequent (B)	29.1	3161	44.9	27	44	29
	Infrequent (C)	22.2	2584	44.2	25	46	28
	Total/Average	75.3	8085	44.8	24	45	31
Bluegrass Ridge	Control (A)	28.3	2509	42.2	25	59	16
	Frequent (B)	31.2	2586	48.8	47	44	09
	Infrequent (C)	49.8	3534	40.1	39	41	20
	Total/Average	109.3	8629	43.1	37	48	15
All Areas	Control	96.9	9523	46.0	25	41	34
	Frequent	123.0	11237	45.1	36	41	24
	Infrequent	121.6	10891	43.2	32	40	29

Table 2.—Summary information of treatment-level landscape features, by IMI class, for each study area (all averages are weighted) except for lengths of streams or ridges.

ITEM	Control			Frequent			Infrequent			Average		
	Xeric	Inter.	Mesic	Xeric	Inter.	Mesic	Xeric	Inter.	Mesic	Control	Frequent	Infreq.
Arch Rock												
IMI	29.4	43.1	63.4	28.8	41.7	64.3	28.8	42.3	57.1	46.3	44.2	39.2
Flow	23.7	30.8	48.9	24.2	29.4	47.1	18.9	35.5	62.3	35.3	33.2	33.3
Hillshade	37.3	60.2	80.8	36.7	62.0	83.3	41.9	58.3	70.8	60.6	59.2	53.6
Curvature	37.3	47.4	54.5	36.1	41.7	51.2	35.7	50.8	65.5	46.8	42.7	47.0
WHC[a] (cm)	2.53	2.93	4.71	2.42	2.60	4.94	2.29	2.40	2.49	3.5	3.3	2.4
Slope (degrees)	15.5	16.7	19.8	17.6	17.5	20.6	14.5	15.5	15.3	17.5	18.5	15.1
Elevation (m)	253.8	247.4	234.6	247.7	246.7	234.6	250.1	247.7	241.1	244.7	243.1	247.5
Minimum	201.2	199.8	199.9	208.2	206.3	209.0	207.8	206.6	207.3	200.3	207.9	207.2
Maximum	281.3	280.7	273.9	279.6	278.4	270.5	280.5	279.5	273.9	278.4	276.3	278.9
Range	80.1	80.9	74.0	71.4	72.2	61.4	72.7	73.0	66.5	78.1	68.3	71.7
Site Index	60.5	66.0	74.4	60.3	65.5	74.7	60.3	65.7	71.8	67.4	66.5	64.5
Streams (m)	0	8	1479	0	16	545	0	58	1203	496	187	420
Ridges (m)	1994	862	533	1553	636	326	2734	548	9	1130	838	1097
Watch Rock												
IMI	28.0	43.4	64.3	29.3	42.6	57.8	28.1	43.5	61.7	50.1	42.3	49.4
Flow	19.0	32.8	54.6	15.2	34.8	62.3	20.4	29.2	49.1	40.3	30.3	37.2
Hillshade	37.0	57.9	75.6	35.7	53.6	68.6	35.7	56.1	68.8	61.8	51.9	58.4
Curvature	35.3	47.3	58.4	37.6	49.2	66.2	37.8	46.2	58.7	50.0	45.6	50.7
WHC[a] (cm)	2.64	3.12	4.96	3.43	3.18	2.94	2.63	3.72	5.47	3.9	3.8	4.4
Slope (degrees)	16.8	18.9	17.1	15.4	15.8	14.2	20.3	17.3	16.1	17.6	16.7	17.3
Elevation (m)	249.5	245.6	223.3	259.4	250.0	240.6	250.7	238.9	223.2	235.6	246.2	233.5
Minimum	204.1	199.5	196.8	218.3	217.5	217.1	201.0	201.0	201.0	199.2	208.0	201.0
Maximum	293.6	292.3	277.3	287.4	280.2	272.0	292.2	291.6	288.4	285.3	285.7	290.2
Range	89.5	92.9	80.6	69.1	62.7	54.9	91.2	90.6	87.4	86.1	77.8	89.2
Site Index	60.0	66.2	74.7	60.5	65.9	72.1	60.0	66.2	73.7	68.9	65.8	68.7
Streams (m)	0	18	1496	0	0	949	0	0	1007	505	316	336
Ridges (m)	1529	661	194	1586	675	0	1035	1195	329	795	754	853

Table 2.—Cont.

ITEM	Control			Frequent			Infrequent			Average		
	Xeric	Inter.	Mesic	Xeric	Inter.	Mesic	Xeric	Inter.	Mesic	Control	Frequent	Infreq.
Youngs Branch												
IMI	29.9	42.8	57.7	30.1	42.7	56.8	30.6	43.2	57.9	45.2	44.9	44.2
Flow	16.3	38.4	65.3	17.8	36.5	62.5	15.2	34.3	61.1	43.1	43.0	37.1
Hillshade	42.0	55.5	69.7	42.8	58.0	71.6	45.7	58.0	70.6	57.6	57.3	58.4
Curvature	42.2	51.8	61.0	40.9	50.3	56.8	39.0	49.4	58.3	53.0	52.0	49.3
WHC[a] (cm)	2.63	2.59	2.66	2.50	2.49	2.52	2.64	2.87	3.07	2.6	2.6	2.9
Slope (degrees)	12.5	12.0	11.5	12.3	13.3	12.6	10.8	12.5	13.5	11.9	11.9	12.4
Elevation (m)	276.3	270.2	264.6	278.3	271.6	263.7	275.8	266.2	254.3	269.5	270.5	265.2
Minimum	243.8	235.3	234.8	241.3	230.1	228.4	223.1	219.6	220.4	236.9	237.2	220.7
Maximum	305.4	301.4	294.8	308.3	306.7	300.0	295.0	295.0	291.3	300.0	300.9	293.9
Range	61.6	66.1	60.0	66.9	76.6	71.5	71.9	75.4	70.9	63.0	63.7	73.2
Site Index	60.7	65.9	72.1	60.8	65.9	71.7	61.0	66.1	72.2	66.9	66.8	66.5
Streams (m)	0	5	2155	0	0	1478	0	0	1215	720	493	405
Ridges (m)	1410	319	21	1667	966	9	1780	762	7	583	881	850
Bluegrass Ridge												
IMI	30.9	43.2	56.4	29.3	42.0	55.1	29.4	42.5	55.7	42.2	48.8	40.1
Flow	12.1	40.2	73.8	19.9	48.0	84.2	22.7	44.2	74.0	38.4	56.8	41.9
Hillshade	55.4	63.0	68.1	45.6	53.6	56.4	43.6	57.9	66.8	61.9	63.3	54.2
Curvature	41.2	51.1	62.6	42.7	52.3	64.2	43.2	50.5	57.7	50.4	56.5	49.1
WHC[a] (cm)	1.74	1.68	1.65	1.69	1.73	1.71	1.71	1.75	1.74	1.7	1.7	1.7
Slope (degrees)	10.5	12.0	10.2	10.9	11.3	10.1	12.2	11.9	11.5	11.4	10.8	11.9
Elevation (m)	242.0	233.7	223.7	255.4	251.6	245.3	252.4	250.8	242.5	234.2	231.3	249.8
Minimum	207.5	204.4	204.2	217.0	211.6	215.3	194.7	196.2	199.7	205.2	206.3	196.4
Maximum	272.0	273.2	268.4	279.9	278.6	269.5	296.4	295.8	292.2	272.1	271.4	295.3
Range	64.5	68.8	64.2	62.8	67.0	54.2	101.6	99.5	92.5	66.9	65.1	98.9
Site Index	61.2	66.1	71.5	60.5	65.6	71.0	60.6	65.8	71.2	65.7	68.4	64.9
Streams (m)	0	44	1081	31	185	1405	11	228	2486	375	540	908
Ridges (m)	1927	420	0	3158	210	8	4200	731	21	782	1125	1651

[a]WHC = Water-holding capacity. Maximum capacity of water (cm) in A and B soil horizons.

Table 3.—Summary information for plot-level landscape, by IMI class, for each study area (all averages are weighted).

	Control			Frequent			Infrequent			Average		
Item	**Xeric**	**Inter.**	**Mesic**	**Xeric**	**Inter.**	**Mesic**	**Xeric**	**Inter.**	**Mesic**	**Control**	**Frequent**	**Infreq.**
					Arch Rock							
IMI	30.0	46.5	62.4	27.9	37.7	73.5	29.7	44.8	53.4	46.3	46.4	42.6
Flow	22	25	42	30	44	50	22	39	37	29	41	33
Hillshade	34	78	88	28	46	90	40	63	85	67	54	62
Curvature	34	41	56	44	64	44	38	51	38	44	51	42
WHC[a] (cm)	2.71	2.24	4.36	2.49	2.07	6.83	2.24	2.43	2.24	3.10	3.79	2.30
Slope, degrees	15	26	21	20	19	23	15	19	19	21	21	17
Aspect, degrees	178	330	1	164	223	15	191	191	36	[b]	[b]	[b]
Elevation, m	259	251	235	248	235	223	259	246	240	249	235	248
D-Streams, m	66	80	57	73	50	111	49	34	60	68	78	48
D-Ridges, m	19	21	31	26	56	58	17	30	28	24	47	25
Est. Site Index, ft	60	67	74	60	64	79	60	67	70	67	68	66
					Watch Rock							
IMI	30.7	37.3	62.4	27.0	42.8	57.9	27.0	47.8	63.4	43.4	42.6	46.1
Flow	16	40	49	17	30	39	18	48	29	35	29	31
Hillshade	39	24	88	21	62	81	31	55	84	50	54	57
Curvature	29	54	57	48	44	54	36	44	46	47	49	42
WHC[a] (cm)	3.04	4.47	3.80	3.37	2.69	4.08	2.72	3.04	6.41	3.77	3.38	4.06
Slope, degrees	13	22	22	19	18	19	19	24	19	19	19	21
Aspect, degrees	174	165	0	207	b	56	169	107	47	[b]	[b]	[b]
Elevation, m	236	218	228	276	244	243	254	222	218	227	254	231
D-Streams, m	78	37	37	66	40	62	48	44	94	51	56	62
D-Ridges, m	13	47	48	8	26	20	17	41	34	36	18	31
Est. Site Index, ft	60	64	74	59	66	72	59	67	74	66	66	67

Table 3.—Cont.

Item	Control			Frequent			Infrequent			Average		
	Xeric	Inter.	Mesic	Xeric	Inter.	Mesic	Xeric	Inter.	Mesic	Control	Frequent	Infreq.
Youngs Branch												
IMI	33.1	46.1	55.2	30.6	43.1	59.9	36.8	40.1	57.2	44.8	44.6	44.7
Flow	35	38	50	31	33	57	17	25	50	41	40	31
Hillshade	34	67	77	33	61	83	30	60	76	59	59	55
Curvature	48	47	50	40	50	53	40	42	52	48	48	45
WHC[a] (cm)	2.67	2.19	2.67	2.53	2.67	2.67	2.37	2.45	3.45	2.51	2.62	2.76
Slope, degrees	15	14	13	15	11	15	16	10	16	14	14	14
Aspect, degrees	186	85	38	210	258	14	199	287	60	[b]	[b]	[b]
Elevation, m	280	277	267	279	268	255	275	284	252	275	267	270
D-Streams, m	64	83	36	79	51	38	35	73	33	61	56	47
D-Ridges, m	28	30	72	31	18	35	5	29	51	43	28	28
Est. Site Index, ft	62	67	71	61	66	73	59	65	72	67	67	65
Bluegrass Ridge												
IMI	32.9	42.3	53.1	31.5	43.2	55.3	29.1	43.6	54.9	42.8	43.4	42.5
Flow	20	35	57	43	43	72	24	37	61	37	53	41
Hillshade	49	65	75	36	59	68	41	66	75	63	54	60
Curvature	43	44	50	49	49	65	41	47	55	46	54	48
WHC[a] (cm)	2.06	1.75	1.63	1.63	1.68	1.64	1.63	1.64	0.10	1.81	1.65	1.63
Slope, degrees	12	12	14	14	13	11	11	16	14	13	13	14
Aspect, degrees	137	*	65	231	165	82	241	92	67	[b]	[b]	[b]
Elevation, m	268	248	222	251	251	261	268	241	239	246	255	249
D-Streams, m	91	70	23	37	45	10	92	53	23	61	31	56
D-Ridges, m	27	20	64	48	33	81	21	33	51	37	54	35
Est. Site Index, ft	62	66	70	62	66	71	60	66	71	66	66	66

[a]WHC = Water-holding capacity. Maximum capacity of water (cm) in A and B soil horizons.
[b]Average aspect not reasonable calculated because of high variability.

holding capacity), the scores increased as moisture level increased. Water-holding capacity was highest at the Vinton County sites, particularly the treatment areas with deep bottomland soils of the Elk Fork (WR CONT and INFR and AR FREQ and INFR). Slope angle also was generally higher at the Vinton County sites, with several treatment units averaging more than 20 degrees in slope. Elevation was highest at YB as several ridgetops exceeded 300 m. The average for the other three sites was 230 to 250 m. As expected, total ridge length was higher for the xeric classes than for the more mesic zones, while stream length was almost exclusively in the latter.

The treatment units generally were equivalent with respect to landscape variables (Table 1). Ideally, the weighted averages among control, frequent, and infrequently burned plots should be similar so that treatment effects can be attributed to the treatment rather than other variables. Similar scores among treatment units is the case in most instances, though there are exceptions. For example, WR FREQ has a lower IMI and flow accumulation than the other treatment units at WR. Given that these are weighted averages, most of the difference is attributed to the disproportionately lower amount of mesic area relative to the other units (25 percent for WR FREQ versus 49 percent for WR CONT and INFR; Table 1).

Landscape Features of Plots

A precise location of the 108 plots allows for a more detailed analysis of the biotic and abiotic factors associated with the landscape features. The plot data also provide information that will allow extrapolation to landscape scales. Reported data are similar to those reported in the previous section for the treatment and IMI classes, but also include estimates of the distances to the nearest ridge and stream as well as estimates of aspect in degrees (Table 3).

The plots are representative of the entire treatment areas, as the mean values for the plots correspond well with the weighted averages for the treatment areas (Tables 2-3). Therefore, we can be confident that the results obtained from plot investigations can be reasonably extrapolated to the entire treatment area and beyond.

At the plot level, the weighted average overall IMI scores were similar among treatments, ranging only from 42.5 for BR INFR to 46.4 for AR FREQ (Table 3). However, variability was higher among the four components used to derive IMI. For example, average flow accumulation is higher for BR FREQ and AR FREQ than for the other treatments because of long hillslopes. Hillshade values were lower on those same units. Because hillshade and flow accumulation account for 70 percent of the IMI score, these variables tend to compensate for each other in the distribution.

Plots classified as xeric tended to be southerly in aspect and higher in elevation, while mesic plots generally faced north and were lower in position. The intermediate plots were intermediate in these traits but varied in average aspect in degrees (some averages were not reasonably calculated due to the high variability among plots). The intermediate plots were on a variety of slopes but often faced east or west.

Plot center distances to the nearest ridge or stream generally were as expected, with xeric plots nearest ridges and mesic plots nearest streams. However, these data were variable and not always easily understood. Because of the extremely dissected nature of the study areas, a plot can be near a stream or ridge horizontally, but not if corrected for slope. The dissected landscape also yielded many small streams or ridgelines so that plots were rarely more than 75 m from either.

Conclusion

The IMI can be developed from readily available topographic data and soils maps. It requires no field assessments, is time invariant (excluding geologic time), and is consistent between areas to be assessed. The IMI is related to site productivity (site index) and to species composition (Iverson et al. 1996, 1997). It also is useful for predicting ecosystem attributes such as understory vegetation patterns (Iverson et al. 1996; Hutchinson et al. 1999), species richness (Hutchinson et al. 1999), soil pH and available nitrogen (Morris and Boerner 1998), root production (Dress and Boerner 2001) and distributions of bird species (Dettmers and Bart 1999). The IMI is recommended as a site attribute for ecosystems where moisture is limiting.

The GIS analysis showed that the plots are highly representative of the entire treatment area, as the mean values of many landscape variables for the plots are similar to the weighted averages for the entire treatment area. Therefore, the results obtained from plot investigations can be reasonably applied to all treatment units. We are confident that the results of our prescribed-burning experiments can be extrapolated to other locations in southern Ohio and beyond.

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Chapter 4

Physiography, Geology, and Soil Classification

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Abstract

The four study areas, located within the Unglaciated Allegheny Plateau of southern Ohio, are underlain predominantly by sandstones and shales of Pennsylvanian Age. The bedrock underlying the Arch Rock (AR), Watch Rock (WR), and Young's Branch (YB) study areas also contain economically important coal strata, while those of the Bluegrass Ridge (BR) study area have significant interbedded limestone layers. The soils include inceptisols, alfisols, and ultisols, and are predominantly loams and silt loams formed in residuum and colluvium. The soils of AR and WR are dominated by the Steinsburg-Gilpin Association, those at YB by soils of the Steinsburg-Shelocta Association, and those at BR by the Upshur-Gilpin-Steinsburg Association.

Physiography and Geology

The study sites are located within the Unglaciated Allegheny Plateau of southern Ohio. Each site is underlain by sedimentary strata of Pennsylvanian age. Although acidic sandstones, shales, and coals comprise the large majority of these strata, narrow, discontinuous bands of limestone are scattered throughout (King 1979). The topography of the region is dominated by highly dissected ridge and valley complexes with relative relief of 90 to 150 m (Gordon 1969). The relative relief is greater and the slopes steeper where relatively erosion-resistant sandstones cap the ridges than where the ridges are capped by the softer shales (King 1979).

The bedrock underlaying the two Vinton County sites — Arch Rock (AR) and Watch Rock (WR) located within the Vinton Furnace Experimental Forest, are members of the Allegheny Group, the most economically important group of strata in Ohio (Denton et al. 1961). Most of this bedrock complex is composed of sandstones and shales of marine origin that are interbedded with several thin layers of limestone and at least six major coal strata. These mineable coal strata account for over half of Ohio's mineable coal reserves. In the portion of Vinton County that includes AR and WR, the bedrock is dominated by Lawrence sandstone, Vanport shale, and Clarion sandstone. Some areas also have small amounts of Vanport limestone (Denton et al. 1961).

Young's Branch (YB), located on a portion of the Wayne National Forest in Lawrence County, is located on bedrocks belonging to the Allegheny group. By contrast, Bluegrass Ridge (BR), the other study area in Lawrence County, is underlain by sedimentary strata of the Connemaugh group. The bedrock complex includes a combination of sandstones, sandy shales (or siltstones), and clay shales (Denton et al. 1961). Significant coal strata are much less common here than in Vinton County as the Connemaugh group accounts for less than 5 percent of Ohio's coal reserves. Interbedded limestone layers appeared more common in the area surrounding BR than near the other study areas. The thickness of these limestone layers varies considerably even over small distances. Thus, the degree to which these limestone layers might influence soil properties depends on the local thickness within each study site.

Soil Series and Complexes

Natural Resource Conservation Service maps for the study areas suggest that the soils of most of the 108 vegetation plots (27 per study area) are dominated by silt loams derived from colluvium and residuum generated by a combination of sandstone, siltstone, and shale (Table 1). Complexes or associations that included Gilpin and/or Steinsburg series soils were mapped as occurring in 98 percent of the vegetation plots at YB and BR. Steinsburg series soils are inceptisols with a shallow, weakly developed, moderately acidic A horizon derived from sandstone (Table 2). At YB and BR, the Steinsburg soils are most common on upper slopes and ridgetops. At YB, the Steinsburg soils often were

associated with ultisols of the Latham and Shelocta series in midslope positions. These latter two soil series have deeper, more developed A horizons than the Steinsburg soils. At BR, the Steinsburg soils most often are associated with Gilpin series soils on mid slopes. Gilpin series soils are well developed ultisols with strongly acidic, shallow A horizons.

There also are areas on mid to upper slopes at BR, particularly in the control unit (CONT), that are underlain by Upshur series soils formed predominantly from limestone. These alfisols have a deeper A horizon and higher pH than the surrounding associated Steinsburg and Gilpin soils, and were easily differentiated in the field on the basis of color and apparent clay content. These scattered pockets of less acidic Upshur alfisols within the matrix of acidic ultisols and inceptisols constitute the primary source of edaphic diversity within BR. At YB, one lower slope vegetation plot is underlain by Stendahl silt loam, an entisol derived from recent alluvium (Tables 1-2).

At AR and WR, nearly 90 percent of the vegetation plots were mapped as Gilpin series soils or as associations with a major Gilpin component (Table 1). At AR and WR, Gilpin ultisols were predominantly on ridgetops and upper shoulder slopes, often in association with Rarden and/or Germano series soils lower on the slopes and Steinsburg series soils on the ridges. Seven of the lower slope vegetation plots at these two study sites are underlain by Chagrin loams. Chagrin soils, inceptisols formed in recent alluvium, have both higher pH and water-holding capacity than the ultisols higher on the slopes. It is likely that vegetation plots underlain by Chagrin series soils will remain moist even during periods of drought in midsummer.

Overall, the soils of the mid to upper slope and ridgetop portions of the four study areas are dominated by acidic ultisols and inceptisols derived from combinations of sandstone, siltstone, and shales. At BR, and perhaps at WR, scattered pockets of alfisols derived from thin, discontinuous limestone beds add significant edaphic diversity. On lower slope positions, soils with high water-holding capacity derived from recent alluvium dominated.

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Table 1—Soil series mapped on 108 vegetation plots in the four study areas (based on USDA Soil Conservation Service maps published by the Ohio Department of Natural Resources).

Site	Lawrence County			
	Upshur-Gilpin-Steinsburg Association	Upshur-Gilpin Association	Steinsburg-Shelocta Association	Latham Steinsburg Complex
Young's Branch	0	0	23	3
Bluegrass Ridge	22	5	0	0
	Vinton County			
	Steinsburg-Gilpin Association	Germano-Gilpin Complex	Gilpin-Rarden Complex	Chagrin Loam
Arch Rock	20	1	1	5
Watch Rock	14	9	2	2

Table 2.—Chemical and physical characteristics of soil series mapped in the study areas. Data adapted from McCleary and Hamilton (1990) and Lemaster and Gilmore (1993).

Soil Series	Parent material	Texture	A-horizon depth	pH	Indicator species
Steinsburg	Sandstone	Loam	5	4.5-5.5	Northern red oak, Yellow-poplar
Gilpin	Sandstone, shale, and siltstone	Loam to silt loam	5	3.6-5.5	Red oak, Yellow-poplar, Virginia pine
Shelocta	Sandstone, shale, and siltstone	Loam to silt loam	10-15	4.5-5.5	Shortleaf pine, Virginia pine, Yellow-poplar
Germano	Siltstone and sandstone	Sandy loam	5-7	3.6-5.5	Northern red oak, Yellow-poplar
Rarden	Siltstone and sandstone	Silt loam to sandy loam	3-6	3.6-5.5	Red, black, and white oak
Latham	Shale and siltstone	Silt loam	5-7	3.5-6.5	Red, white, and black oak, Virginia and shortleaf pine
Upshur	Limestone	Loam to silt loam	5-10	4.5-6.5	Yellow-poplar, Redbud
Chagrin	Alluvium	Loam	25	5.6-7.3	Red and white oak, Sugar maple, Black cherry
Stendal	Alluvium	Silt loam	25	4.5-6.5	Pin oak, Sweetgum, Yellow-poplar, White ash, Slippery elm

Chapter 5

Soil and Forest Floor Characteristics

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Abstract

The soils of the four study areas in southern Ohio were dominated by silt loams derived from sandstones and shales. The soils at Bluegrass Ridge (BR) had significantly more clay and sand and significantly less silt than soils of the other study areas. Total inorganic N (TIN) and available NH_4 were greatest in soils from Watch Rock (WR) and least at Young's Branch (YB). TIN, NH_4, and NO_3 availability varied directly with Integrated Moisture Index (IMI). Soil pH, PO_4, Ca, Mg, and molar Ca:Al ratio also varied among sites; soils from Arch Rock (AR) had the lowest pH, Ca, Mg, and Ca:Al ratio while those from BR had the highest. Al and pH varied with IMI as soils from xeric plots had the lowest pH and the highest soluble Al levels. The availability of PO_4, Ca, and Mg and the Ca:Al ratio were lower in soils from xeric plots than from intermediate and mesic plots. Unconsolidated litter mass averaged 438 g/m^2 and did not differ significantly among treatment units or IMI classes. Litter mass was greatest at YB, averaging 527 g/m^2. Detrended Correspondence Analysis indicated that a strong pH/mineral availability gradient was the primary factor that influenced soil chemistry among the study 108 plots. Mesic plots from BR and WR separated in the ordination from the remainder of the sample plots, suggesting that these plots may not be as useful as the remaining plots for detecting subsequent fire effects on soils and belowground processes.

Introduction

The physiography and parent materials within the Unglaciated Allegheny Plateau of southern Ohio control the physiochemical characteristics and rates and patterns of nutrient cycling in soil of forested watersheds when major disturbances are rare (Finney et al. 1962; Boerner 1985). Portions of some watersheds in this region are underlain by limestone. These areas generate soils that are significantly higher in pH and base cations than those underlain by the region's widespread and relatively acidic sandstones, shales, and coals. Because forest productivity often varies as a function of soil nutrient availability and species distributions often are correlated with the presence or absence of limestone, a significant proportion of the heterogeneity observed in the forested landscape of southern Ohio can be attributed to occasional limestone outcrops (see Chapter 4).

In areas underlain by relatively acidic sandstones and shales, as is the case for most of our 108 study plots, differences in microclimate among slope positions and aspects generate differences in soil development, horizon depth, accumulation of organic matter, and rates of decomposition. This results in greater soil-horizon development and nutrient availability and lower decomposition rates on south- and west-facing slopes than on the more mesic north- and east-facing slopes (Finney et al. 1962; Hutchins et al. 1976; Boerner 1984). As a result, N mineralization rate and nitrification, the processes that convert organic N into forms available for tree use, also are greater on mesic slopes (Plymale et al. 1987).

Despite small differences in the annual rate of leaf, branch, and litter deposition among stands within watersheds, patterns of leaf litter redistribution following litterfall result in the ridgetops and drier south- and west-facing slopes serving as net donors of organic matter and nutrients to the more mesic north- and east-facing slopes (Welbourn et al. 1981; Boerner and Kooser 1989). Thus, nutrients taken up from the soil by trees on the drier slopes and ridgetops may be deposited in detritus and recycled on mesic slopes (Boerner and Kooser 1989). Gradients of soil-nutrient availability and nutrient cycling rates are thus maintained in these physiographically diverse watersheds by a combination of geological, microclimatological and ecological processes.

Leaf litter also plays an important role in plant communities (Facelli and Pickett 1991). By serving as a mechanical barrier, leaf litter can hinder the emergence of tree seedlings (Myster 1994) and forbs (Bosy and Reader 1995), which, in turn, reduces species richness (Beatty and Sholes 1988).

In this chapter we document variations in physiochemical characteristics of the soil and the forest floor in the four study areas prior to the reintroduction of surface fires. Specifically, we characterize the current ecological status of these soils and draw inferences concerning variations in soil physiochemical status among study areas and treatment units in relation to aspect- and elevation-driven differences in microclimate.

Methods

Study Areas and Experimental Design

The study areas and experimental design are described in detail in Chapter 1. Here a brief overview is provided. The four 75-90 ha study areas are located in Vinton County (Arch Rock and Watch Rock) and Lawrence County (Young's Branch and Bluegrass Ridge). The study areas are within in the Southern Unglaciated Allegheny Plateau, which is characterized by high hills, sharp ridges, and narrow valleys. Sandstones and shales are principle bedrocks. Forests are oak-dominated and the current overstory originated in the late-1800s, after the cessation of clearcutting for the charcoal iron industry.

In each study area, three prescribed fire treatments were established, a control unit (CONT), an infrequent burn unit (INFR), and a frequent burn unit (FREQ). To account for variation in soil moisture and vegetation, a GIS-derived integrated moisture index (IMI) was applied across the dissected landscapes of the study areas (Chapter 3). From the calculated IMI scores, each 30 x 30 m pixel was assigned to one of three soil moisture classes: xeric, intermediate, or mesic. Thus to examine the effects of prescribed fire and account for environmental heterogeneity, a split-plot experimental design was established. The four study areas are replicate blocks, fire treatment units are whole plots, and IMI classes are subplots. The 50 x 25 m vegetation plots (N= 108 total) were established as pseudoreplicates in each IMI class within each fire treatment unit (Chapter 1).

Field and Laboratory Methods

In October and November 1994, bulk soil samples were obtained for initial soil characterization. Two A-horizon samples of approximately 1 kg were obtained from randomly selected points 1 to 2 m outside the upper and lower boundaries of each vegetation plot. The bulk soil samples were air dried for approximately 14 days and then passed through a 6-mm sieve to remove roots, wood fragments, and large gravel.

Soil texture was determined on 40-g (dry mass) subsamples from each sieved sample by the hydrometer method; sodium hexametaphosphate was used to disperse carbonates. Soil pH was determined in 1:5 soil: 0.01 M $CaCl_2$ slurries. Subsamples of 10 g were extracted with 2 M KCl for subsequent analysis of NO_3, NH_4, and Al, and with 1 M NH_4OAC for subsequent analysis of Ca, Mg by atomic absorption, and PO_4 by the stannous chloride method. All methods follow Page et al. (1982). Total inorganic N (TIN) was calculated as the sum of NO_3 and NH_4; the Ca:Al ratio was expressed on a molar basis.

In 1996, six leaf litter samples were collected per vegetation plot 1 m from each plot corner in March and April. A square metal frame (0.0225 m^2) with a cutting edge was used to obtain the samples. Because the long-term goal is to examine litter dynamics in response to prescribed fire, not all forest floor layers were collected. The entire L layer was collected, as was litter larger than 2 by 2 cm in the F layer. Smaller pieces in the F-layer, litter that was matted together (partially decomposed), and in the H layer were not collected as these components were not expected to burn in a prescribed fire. Twigs less than 0.5 cm in diameter were collected, but larger twigs, pieces of bark, and nuts were not. The samples were placed in plastic bags, transferred to paper bags and placed in a drying oven within 5 days, and dried at 70°C for 48 hr prior to weighing.

Data Analysis

Percentages of sand, silt, and clay, pH, minerals, litter mass, and inorganic N forms were compared among study areas, treatment units within study areas, and IMI classes within areas by analysis of variance (ANOVA) for a split plot, mixed-factor design with maximum likelihood estimators (Proc Mixed, ML option) using SAS (1994). All data were tested for normality prior to ANOVA, and none required transformation to fit the assumptions of the analysis. Detrended Correspondence Analysis (DCA; PC-Ord 3.0) was used to compare the soils of all 108 vegetation plots using 12 physical and chemical variables simultaneously (Hill and Gauch 1980).

Results

Silt loams dominated the bulk soil samples: 79 percent of the 216 samples analyzed were silt loams. Loams accounted for 14 percent and clay loams 7 percent. A single sample of sandy clay loam was collected at BR. Textural diversity was low at all study areas except BR. In the other study areas, nearly 85 percent of all soil samples were silt loams, while the soils at BR were distributed more evenly among textural

Table 1.-Results of mixed-model ANOVA for soil characteristcs (ns=not significant).

Item	Study area	Unit	IMI class	Unit* IMI Class
Sand	p<0.0008	ns	p<0.0209	ns
Silt	p<0.0011	ns	p<0.0124	ns
Clay	p<0.0033	ns	p<0.0252	ns
PH	p<0.0056	ns	p<0.0001	ns
NH_4	p<0.0001	ns	p<0.0001	ns
NO_3	ns	ns	p<0.0054	ns
TIN	p<0.0425	ns	p<0.0001	ns
PO_4	p<0.0001	ns	p<0.0001	ns
Ca	p<0.0001	ns	p<0.0001	ns
Mg	p<0.0001	p<0.03	p<0.0001	ns
Al	ns	ns	p<0.0001	ns
Ca:Al ratio	i<0.0051	ns	p<0.0064	ns
Litter mass		ns	ns	ns

Table 2.-Percent sand, silt, and clay in A-horizon soils of the four study areas and relative to IMI class (standard errors in parentheses).

					IMI Class		
Item	Arch Rock	Watch Rock	Bluegrass Ridge	Young's Branch	Xeric	Intermediate	Mesic
Sand	25.4a (0.8)	25.6a (0.6)	33.6b (0.8)	27.0a (0.9)	28.2b (0.9)	29.7b (0.7)	25.7a (0.7)
Silt	61.9b (1.0)	61.9b (1.0)	50.6a (1.2)	59.7b (1.3)	57.9a (1.3)	55.9a (1.1)	61.8b (0.9)
Clay	12.6a (0.3)	12.6a (0.4)	15.9b (0.5)	13.3a (0.5)	13.9a (0.4)	14.4b (0.4)	12.5a (0.3)

Note: Means followed by the same letter not significantly different (p>0.05).

classes (46 percent silt loams, 37 percent loams, 15 percent clay loams, and 2 percent sandy clay loams).

The proportions of sand, silt, and clay varied significantly among study areas (Table 1). Soils from BR had significantly more sand and clay and significantly less silt than soils from the other study areas (Table 2). There were no significant differences in textural classes among treatment units, but there were significant differences in soil textural classes among IMI classes (Table 1). Mesic vegetation plots had significantly less sand and more silt than intermediate and xeric plots. Intermediate plots had the most clay content (Table 2).

There were significant differences both among study areas and IMI classes in extractable NH_4 and TIN while extractable NO_3 differed significantly only among IMI classes (Table 1). NH_4 concentrations were greatest in soils from WR and lowest in soils from YB (Table 3). TIN also was greatest in soils from WR exceeding TIN in soils of the other study areas by an average of 69 percent.

Concentrations of NO_3 and NH_4 were significantly lower in soils from the xeric plots than in soils from intermediate and mesic plots (Table 3). TIN availability increased from xeric to intermediate to mesic plots; mean TIN concentrations differed significantly among all three IMI classes.

Soil pH, extractable PO_4, Ca, Mg, and molar Ca:Al ratio all differed significantly among both study areas and IMI classes; extractable Al differed significantly only among IMI classes (Table 1). Soils from AR had the lowest mean pH and those from BR had the highest (Table 3). Soils from YB and BR had significantly greater concentrations of extractable PO_4 than soils from AR and WR (Table 3).

Soils from BR had greater extractable concentrations/ratios of Ca, Mg, and molar Ca:Al than those from the other study areas (Table 3). Variations in Ca availability

Table 3.-Chemical properties of A-horizon soils of the four study areas and relative to IMI class (standard errors in parentheses).

					IMI class		
Item[a]	Arch Rock	Watch Rock	Bluegrass Ridge	Young's Branch	Xeric	Intermediate	Mesic
NH_4	11.59b (1.04)	15.07a (1.51)	11.85b (0.75)	8.20c (0.70)	6.96a (0.56)	12.92b (0.78)	14.78b (1.12)
NO_3	1.42a (0.42)	8.07a (2.27)	2.57a (0.90)	5.37a (1.36)	0.50b (0.14)	3.49b (0.86)	8.85a (1.77)
TIN	13.01a (1.29)	23.14b (2.83)	14.42a (1.23)	13.57a (1.86)	7.47c (0.61)	16.41b (1.25)	23.63a (2.17)
pH	3.92a (0.06)	4.13ab (0.12)	4.43c (0.09)	4.34bc (0.12)	3.75b (0.07)	4.33a (0.08)	4.49a (0.09)
PO_4	0.13b (0.01)	0.10b (0.01)	0.22a (0.01)	0.25a (0.02)	0.12a (0.01)	0.21b (0.02)	0.19b (0.01)
Ca	249.0b (38.2)	408.5b (79.0)	2425.2a (268.6)	593.0b (81.2)	461.9a (136.1)	1305.8b (198.6)	943.7b (132.1)
Mg	61.6b (8.9)	84.1b (12.8)	319.1a (25.7)	71.9b (7.8)	76.8a (14.6)	185.5b (21.5)	134.2b (15.7)
Al	231.8a (21.5)	220.9a (23.9)	172.9a (31.0)	174.6a (23.5)	358.7a (21.8)	154.9b (17.7)	100.3c (12.9)
Ca:Al Ratio	24.4a (13.1)	134.8ab (44.7)	359.2c (96.9)	226.3b (89.5)	67.5b (41.0)	235.8a (58.1)	238.3a (74.9)
Litter mass	414.2 (22.9)	382.5 (17.0)	421.2 (14.9)	527.9 (30.0)	442.2a (35.2)	439.7a (34.9)	425.2a (35.1)

[a] Except for pH and CA:Al ratio, all items are in mg/kg/soil.

were more important than variations in Al in determining inter-area differences in Ca:Al ratio.

There were two general patterns of variation in pH and mineral availability among IMI classes. Al and pH varied linearly with IMI class. Soils from xeric plots had the greatest Al concentrations and the lowest pH (Table 3). By contrast, for PO_4, Ca, Mg, and Ca:Al ratio, availability/ratio was lower in soils from xeric plots than in soils from intermediate and mesic plots. However, levels did not differ significantly between soils from intermediate and mesic plots (Table 3).

Unconsolidated leaf litter was predominantly from oaks, which dominated the overstory in most plots (Chapter 9). Litter mass averaged 437 g/m^2 per plot. There were no significant differences in litter mass among IMI classes; litter mass averaged 442, 440, and 425 g/m^2 on xeric, intermediate, and mesic plots, respectively (Table 3). Although there was substantial variation in mean litter mass among units (239 to 677 g/m^2; Appendix), differences were not significant by treatment (Table 1). YB had the greatest litter mass, averaging 528 g/m^2, while litter mass at the other study areas averaged 383 to 421 g/m^2.

Detrended Correspondence Analysis

We used DCA to compare all soil variables in all soil samples simultaneously. DCA arrayed the samples in two-dimensional space such that the distances between the points representing the various samples were proportional to the degree of overall physiochemical similarity. We performed this analysis to determine similarities among soils of the 108 vegetation plots when all of the properties we measured were compared simultaneously.

DCA spread out the vegetation plots along a first axis that accounted for 63.5 percent of the summed eigenvalues of the ordination (Fig. 1). The second axis accounted for an additional 29.2 percent of the summed eigenvalues, but produced significant spread of points only at the upper end of axis one. Thus, on the basis of soil chemical and textural properties, DCA arrayed the vegetation plots in a triangular cloud.

When the ordination points corresponding to vegetation plots were displayed by study area, it was apparent that the ordination had separated the plots from AR and WR at the lower end of axis 1 from the BR and YB plots at the upper end. Similarly, when the sample points were labeled by IMI class, it was clear that the dry plots clustered at the lower end of axis 1, and the intermediate and mesic plots separated along axis 2 at the upper end of axis 1 (Fig. 1).

Axis 1 scores were strongly, positively correlated with soil pH, inorganic N forms, Ca, Mg, and Ca:Al ratio, and strongly, negatively correlated with available Al (Table 4). Thus, the AR and WR xeric plots at the lower end of axis 1 were predominantly those with high Al, low pH, and low nutrient availability, whereas the more nutrient rich, less acidified soils from the BR and YB intermediate and mesic plots were at the upper end of axis 1.

Axis 2 scores were positively correlated with IMI and available N and negatively correlated with pH and mineral nutrient availability (Table 4). Thus, the plots arrayed at the upper end of axis 2, particularly those from mesic plots at YB and WR, represented the moistest plots and those with the greatest N availability. Those arrayed lower on axis 2 represented intermediate plots, primarily at BR, with high mineral nutrient availability.

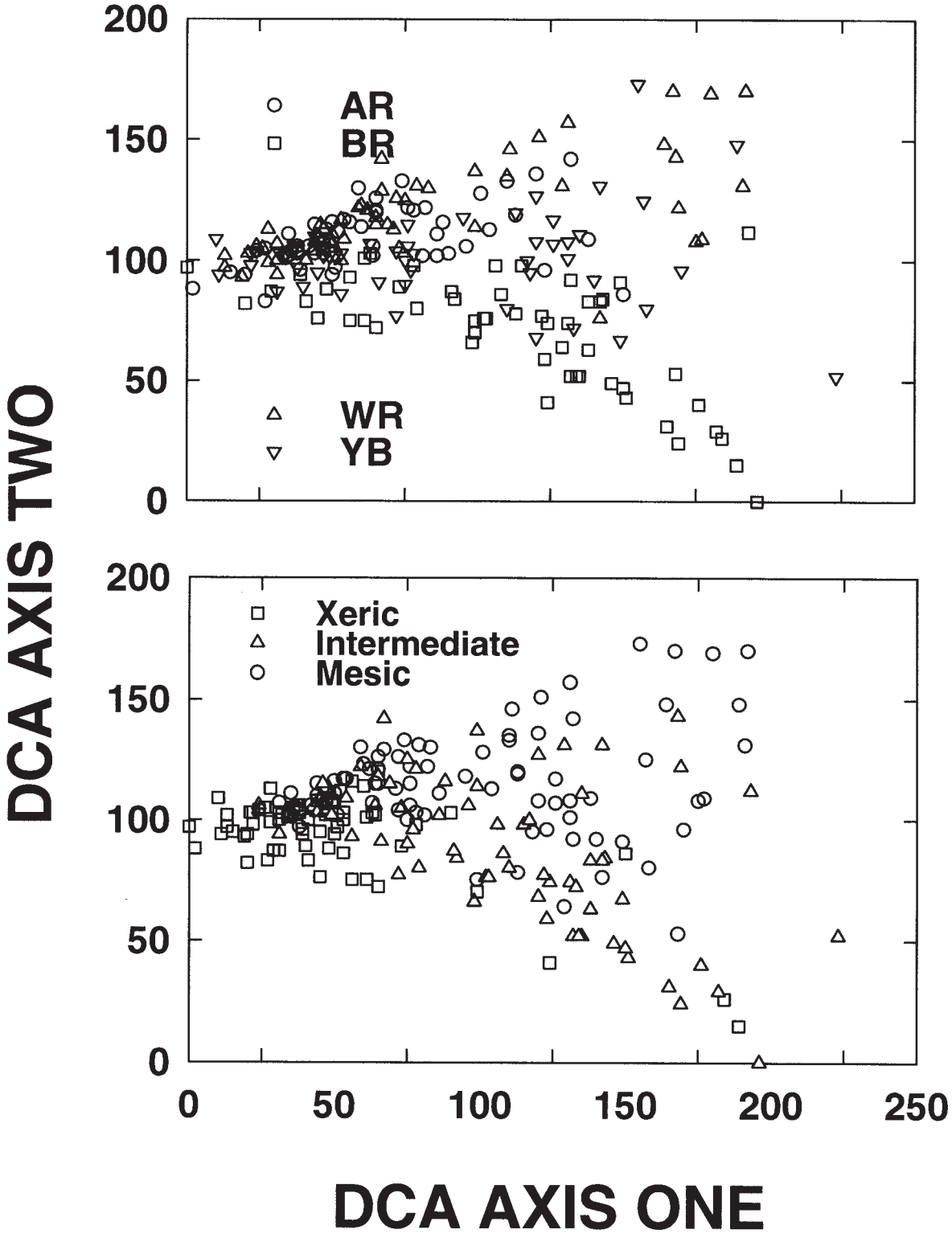

Figure 1.—Detrended Correspondence Analysis ordination of soils from 108 vegetation plots arrayed on the basis of study area (top) and IMI class (bottom).

Table 4.-Pearson Product-Moment correlations between soil factors and DCA ordination axis scores (only correlations significant at p≤0.05 listed).

Item	Axis 1	Axis 2
pH	0.864	-0.181
PO_4	0.514	-0.304
NH_4	0.424	0.338
NO_3	0.609	0.391
TIN	0.677	0.471
Ca	0.723	-0.675
Mg	0.703	-0.635
Al	-0.841	ns
Ca:Al	0.638	-0.419
Sand (%)	ns	-0.550
Clay (%)	ns	-0.520
IMI	0.405	0.315

Discussion

Most of the soils of the four study areas can be characterized as silt loams of colluvial and residual origin with relatively low pH and nutrient availability. However, we also found some vegetation plots with significantly greater pH, Ca, and Mg availability, particularly at BR. These plots probably reflect the influence of the scattered, discontinuous limestone strata that are found within the sandstone and shale matrix of the region (Chapter 4).

The influences of topography, aspect, and slope angle/shape on soil chemical properties were integrated in this study through the use of the IMI; pH and nutrient availability were lower and soluble Al higher in the soils on the driest vegetation plots. Several chemical parameters (e.g., TIN, pH, Al) varied linearly with IMI class, whereas others were similar in soils from intermediate and mesic plots. The texture, chemical properties, and intrawatershed variations of the soils of the study areas generally were consistent with and representative of those of a larger area of the Unglaciated Appalachian plateau of Ohio and Kentucky (Finney et al. 1962; Hutchins et al. 1976; Boerner 1984, 1985).

The inorganic N:P ratio in the soils from the study areas ranged from about 60:1 at BR, YB, and AR to 240:1 at WR. NO_3 accounted for 11 to 18 percent of TIN at AR and BR versus 35 to 40 percent at WR and YB. Such significant concentrations of NO_3 typically accumulate in forest soils when the supply of inorganic N from mineralization plus deposition exceeds the uptake capacity of microbes and plants (van Miegrot et al. 1992). These data suggest that the forests of southern Ohio have become strongly enriched in N due to fire suppression and atmospheric deposition (NADP/NTN 1992, 1993), and may no longer be N limited.

Mean Ca:Al molar ratios for the study areas ranged from 24:1 at AR to 360:1 at BR. However, in the driest vegetation plots at AR and WR, the Ca:Al ratio was commonly below 1.0. Several studies of forest decline have demonstrated significant impacts on growth and foliar nutrient concentrations for a range of tree species when the Ca:Al molar ratio drops below 5.0 (Cronan and Grigal 1995). Matzner (1989) observed nutrient deficiencies developing in European conifer stands when the Ca:Al ratio dropped to 5.0 or below, and Huttermann and Ulrich (1984) concluded that Ca:Al ratio was the best available predictor for forest decline in Scandinavian conifer forests. Additional research is needed to determine whether tree growth and/or nutrient dynamics are being affected by the existing Ca:Al balance in the soils of the study areas, and how repeated burning might cause those ratios to shift.

Leaf litter was distributed evenly across the landscapes of the study areas. Likewise, tree basal area did not differ significantly among treatments or IMI classes (Chapter 9). However, large standard deviations indicate high inter-plot variability unrelated to treatment units and IMI classes. This variability might be related to subtle microtopographic variations and litter redistribution (Boerner and Kooser 1989). YB had more litter, indicating higher litterfall and/or slower rates of litter decomposition. Mean forest-floor litter mass was about 1.5 fold greater than annual litterfall in oak forests of similar age in Hocking County, Ohio (Boerner and Kooser 1989). This finding suggests that a portion of litterfall remains unconsolidated into the F and H layers each year. The baseline data presented here will be useful in determining the dynamics of litter in response to prescribed burning.

DCA ordination identified a large cluster of sample plots with similar soil characteristics. These included most of the vegetations plots at AR and YB and a subset of those at WR and BR. The use of plots with similar soil characteristics will aid in detecting subtle fire effects, particularly in relation to IMI. The ordination also identified a smaller set of high N plots at WR and high Ca and N plots at BR as unique. This subset will be particularly useful in evaluating the influence of variations in underlying edaphic properties on the response of vegetation and ecosystem processes to fire.

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Appendix.--Soil chemical and physical properties of treatment units by IMI category for each study area (standard errors in parentheses).

	Frequent			Control			Infrequent		
Item	**Xeric**	**Intermediate**	**Mesic**	**Xeric**	**Intermediate**	**Mesic**	**Xeric**	**Intermediate.**	**Mesic**
				ARCH ROCK					
Sand (%)	23.4 (1.3)	24.8 (1.8)	23.0 (1.2)	30.6 (3.6)	26.0 (4.0)	23.9 (2.1)	28.3 (2.6)	27.7 (1.4)	23.2 (2.1)
Silt (%)	64.9 (1.6)	63.5 (1.6)	64.7 (1.5)	55.0 (4.9)	60.5 (4.5)	64.6 (2.4)	57.7 (4.1)	58.3 (2.2)	64.8 (2.5)
Clay (%)	11.8 (0.5)	11.8 (0.3)	12.3 (0.3)	14.3 (1.4)	13.5 (0.5)	11.5 (0.5)	14.0 (1.5)	14.0 (0.8)	12.0 (0.8)
pH	3.98 (0.22)	3.70 (0.19)	4.23 (0.15)	3.61 (0.09)	3.76 (0.14)	3.89 (0.11)	3.64 (0.10)	4.06 (0.19)	4.21 (0.26)
NH_4 (mg/kg soil)	7.22 (1.27)	11.79 (3.99)	21.19 (3.54)	7.83 (2.25)	5.19 (2.47)	12.43 (1.91)	7.78 (2.66)	13.55 (2.89)	13.93 (4.51)
NO_3 (mg/kg soil)	1.30 (1.07)	0.23 (0.04)	3.39 (0.77)	0.17 (0.04)	0.17 (0.06)	1.94 (1.70)	0.11 (0.05)	1.08 (0.88)	2.88 (1.59)
TIN (mg/kg soil)	8.52 (1.92)	12.02 (4.02)	24.68 (3.69)	8.01 (2.27)	5.35 (2.41)	14.37 (3.12)	7.89 (2.68)	14.63 (2.45)	16.81 (5.84)
PO_4 (mg/kg soil)	0.12 (0.03)	0.14 (0.04)	0.20 (0.03)	0.14 (0.03)	0.04 (0.01)	0.11 (0.02)	0.08 (0.01)	0.15 (0.03)	0.13 (0.03)
Ca (mg/kg soil)	321.3 (143.0)	110.8 (76.8)	429.2 (64.5)	174.8 (71.3)	18.3 (9.9)	155.4 (79.0)	97.7 (38.6)	414.8 (111.8)	357.7 (164.8)
Mg (mg/kg soil)	62.8 (22.0)	36.3 (10.6)	113.0 (22.1)	38.2 (11.0)	15.3 (4.0)	31.4 (9.1)	36.5 (6.6)	118.5 (53.5)	83.5 (29.2)
Al (mg/kg soil)	180.5 (33.7)	255.2 (50.2)	93.9 (29.6)	433.3 (62.4)	262.9 (70.3)	213.9 (34.6)	371.1 (75.3)	182.6 (68.1)	150.7 (59.7)
Ca:Al ratio	74.5 (73.5)	0.5 (0.4)	11.3 (7.7)	0.3 (0.1)	0. 1 (0.1)	13.1 (12.6)	0.2 (0.1)	16.4 (13.3)	69.9 (64.3)
Litter mass (g/m^2)	392.4 (31.0)	239.1 (70.2)	316.6 (16.7)	539.3 (105.6)	494.8	488.1 (58.0)	451.3 (52.5)	409.7 (21.4)	349.9 (18.3)
				BLUEGRASS RIDGE					
Sand (%)	18.0 (3.0)	30.6 (1.4)	32.5 (2.5)	35.3 (1.2)	38.0 (1.1)	36.5 (1.5)	34.0 (3.0)	35.5 (2.6)	34.3 (1.8)
Silt (%)	70.5 (3.5)	54.9 (2.1)	52.5 (1.5)	48.5 (2.4)	42.9 (2.5)	46.0 (2.0)	48.7 (5.1)	49.3 (3.3)	50.8 (2.4)
Clay (%)	11.5 (0.5)	14.5 (0.8)	15.0 (1.0)	16.3 (1.1)	19.1 (1.6)	17.5 (0.5)	17.3 (2.2)	15.2 (0.8)	14.8 (0.7)
pH	3.80 (0.19)	4.51 (0.16)	4.66 (0.36)	4.19 (0.29)	4.50 (0.24)	5.27 (0.08)	3.71 (0.15)	4.72 (0.26)	4.72 (0.23)
NH_4 (mg/kg soil)	6.80 (1.79)	13.92 (1.24)	15.81 (0.02)	8.17 (1.77)	11.8 (1.82)1	20.76 (4.21)	6.80 (0.68)	14.28 (2.47)	12.01 (2.20)
NO_3 (mg/kg soil)	0.28 (0.01)	5.04 (3.20)	7.30 (7.30)	0.85 (0.47)	1.04 (0.43)	1.77 (1.27)	0.27 (0.06)	1.73 (0.80)	3.75 (1.52)
TIN (mg/kg soil)	7.08 (1.80)	18.96 (3.29)	23.10 (7.28)	9.03 (2.15)	12.85 (1.91)	22.53 (5.48)	7.06 (0.70)	16.01 (2.49)	15.76 (2.93)
PO_4 (mg/kg soil)	0.14 (0.01)	0.25 (0.01)	0.24 (0.04)	0.17 (0.03)	0.24 (0.03)	0.25 (0.04)	0.18 (0.03)	0.22 (0.04)	0.24 (0.04)
Ca (mg/kg soil)	858.2 (610.5)	2198.9 (312.5)	2278.6 (341.8)	1805.8 (915.5)	2781.0 (1011.1)	5020.6 (495.7)	1259.9 (446.0)	3761.4 (955.3)	2839.8 (466.5)
Mg (mg/kg soil)	111.0 (52.5)	293.4 (29.2)	368.3 (63.6)	228.6 (89.8)	350.6 (79.0)	439.4 (20.5)	216.2 (48.7)	487.5 (93.5)	405.3 (57.7)
Al (mg/kg soil)	182.5 (39.3)	76.0 (21.8)	26.8 (21.3)	349.7 (99.0)	196.5 (81.3)	3.3 (1.4)	518.0 (96.4)	44.8 (21.6)	30.6 (16.5)
Ca:Al ratio	3.8 (3.1)	170.7 (83.7)	174.8 (147.7)	533.2 (343.6)	527.2 (407.1)	1310.9 (664.2)	6.1 (5.1)	627.8 (330.6)	288.2 (194.0)
Litter mass (g/m^2)	386.4 (20.0)	438.3 (11.7)	524.4	299.3	472.8 (27.8)	376.3	443.2 (35.3)	322.2 (30.2)	422.4 (60.3)

Appendix cont.

Item	Frequent			Control			Infrequent		
	Xeric	Intermediate	Mesic	Xeric	Intermediate	Mesic	Xeric	Intermediate.	Mesic
				WATCH ROCK					
Sand (%)	26.5 (1.4)	24.2 (1.4)	25.0 (2.2)	28.5 (3.2)	24.5 (2.0)	25.4 (1.3)	27.3 (2.8)	26.3 (0.3)	23.9 (1.5)
Silt (%)	62.0 (1.9)	63.6 (2.0)	62.3 (4.4)	56.8 (4.9)	63.0 (2.9)	61.8 (2.3)	59.3 (3.7)	60.8 (0.5)	65.1 (1.7)
Clay (%)	11.5 (0.5)	12.2 (0.8)	12.8 (2.3)	14.7 (1.8)	12.5 (0.9)	12.9 (1.1)	13.3 (1.2)	13.0 (0.4)	11.0 (0.6)
pH	4.21 (0.77)	3.83 (0.11)	3.53 (0.11)	3.43 (0.08)	3.93 (0.27)	4.18 (0.20)	3.53 (0.05)	5.03 (0.46)	5.31 (0.23)
NH_4 (mg/kg soil)	8.53 (1.52)	16.30 (3.29)	13.32 (3.98)	6.59 (0.80)	15.00 (3.18)	24.75 (7.17)	10.64 (3.80)	20.03 (3.39)	15.40 (1.55)
NO_3 (mg/kg soil)	0.17 (0.06)	1.10 (0.81)	0.17 (0.14)	0.14 (0.03)	3.05 (2.57)	4.42 (1.84)	0.43 (0.25)	15.43 (8.71)	37.99 (8.19)
TIN (mg/kg soil)	8.70 (1.58)	17.40 (3.77)	13.49 (3.98)	6.73 (0.80)	18.06 (5.60)	29.17 (8.28)	11.07 (4.04)	35.45 (7.35)	53.38 (7.53)
PO_4 (mg/kg soil)	0.07 (0.02)	0.09 (0.02)	0.06 (0.02)	0.07 (0.01)	0.08 (0.03)	0.11 (0.02)	0.08 (0.02)	0.15 (0.02)	0.18 (0.01)
Ca (mg/kg soil)	93.2 (41.3)	159.5 (54.9)	86.2 (30.5)	86.1 (51.2)	287.5 (186.8)	410.9 (173.5)	54.5 (24.0)	794.4 (367.0)	1323.0 (213.0)
Mg (mg/kg soil)	47.9 (15.1)	49.2 (11.0)	42.1 (14.5)	28.5 (7.0)	70.5 (25.8)	107.0 (40.9)	27.5 (4.3)	184.4 (89.3)	184.7 (34.3)
Al (mg/kg soil)	460.3 (40.6)	222.7 (50.2)	253.4 (46.5)	438.2 (57.7)	208.0 (65.2)	117.5 (27.6)	275.6 (60.3)	146.4 (83.7)	26.0 (24.0)
Ca:Al ratio	0.1 (0.0)	2.7(1.8)	0.3 (0.1)	0.2 (0.1)	10.4 (10.1)	97.5 (92.5)	1.9 (1.8)	238.6 (145.9)	649.7 (180.7)
Litter mass (g/m^2)	357.8 (123.7)	370.8 (48.2)	299.1 (38.7)	363.6 (28.6)	403.4 (74.4)	349.1 (27.1)	504.5 (51.3)	426.9 (23.2)	375.0 (30.7)
				YOUNG'S BRANCH					
Sand (%)	25.8 (3.7)	30.7 (1.1)	23.8 (1.0)	25.7 (3.3)	27.7 (3.9)	25.4 (1.6)	26.0 (3.6)	32.2 (3.0)	25.8 (2.1)
Silt (%)	61.8 (4.6)	54.0 (1.5)	64.0 (1.5)	60.7 (4.7)	60.0 (5.3)	62.8 (2.5)	61.0 (5.1)	51.3 (5.6)	62.0 (3.0)
Clay (%)	12.3 (1.0)	15.3 (0.6)	12.2 (0.5)	13.7 (1.5)	12.3 (1.5)	11.9 (1.0)	13.0 (1.5)	16.3 (2.9)	12.3 (1.1)
pH	3.52 (0.06)	4.40 (0.31)	4.53 (0.19)	3.63 (0.52)	4.79 (0.45)	4.95 (0.21)	3.69 (0.03)	4.30 (0.20)	4.90 (0.32)
NH_4 (mg/kg soil)	3.62 (0.09)	8.95 (1.77)	9.96 (2.58)	3.66 (0.52)	7.80 (1.55)	10.66 (1.06)	5.39 (1.04)	10.08 (3.60)	10.89 (1.92)
NO_3 (mg/kg soil)	0.47 (0.11)	1.70 (2.17)	12.72 (6.00)	0.56 (0.14)	3.98 (2.03)	10.04 (3.06)	0.68 (0.03)	2.59 (1.72)	10.79 (6.40)
TIN (mg/kg soil)	4.09 (0.16)	10.64 (2.17)	22.67 (8.11)	4.22 (0.41)	11.79 (2.71)	20.70 (3.21)	6.07 (1.05)	12.67 (5.29)	21.68 (7.96)
PO_4 (mg/kg soil)	0.14 (0.03)	0.43 (0.09)	0.29 (0.05)	0.12 (0.03)	0.24 (0.09)	0.27 (0.04)	0.15 (0.07)	0.29 (0.08)	0.25 (0.03)
Ca (mg/kg soil)	69.7 (20.5)	808.3 (313.0)	628.8 (151.0)	100.6 (40.6)	919.3 (396.6)	884. 0 (158.1)	108.5 (62.5)	807.0 (273.7)	899.1 (391.4)
Mg (mg/kg soil)	20.6 (6.2)	92.0 (17.9)	61.9 (9.6)	23.5 (6.1)	82.5 (16.2)	92.6 (16.3)	33.6 (14.3)	125.2 (41.7)	97.6 (19.2)
Al (mg/kg soil)	325.9 (47.5)	166.6 (75.1)	57.9 (31.4)	405.9 (51.3)	72.1 (64.2)	28.4 (23.2)	332.6 (57.4)	152.5 (57.0)	79.4 (39.7)
Ca:Al ratio	0.18 (0.07)	163.1 (141.3)	168.5 (85.1)	0.17 (0.05)	142.9 (123.9)	800.7 (547.2)	0.2 (0.1)	43.7 (26.8)	391.4 (148.1)
Litter mass (g/m^2)	546.4 (60.5)	600.4 (48.0)	548.8 (33.9)	374.4 (3.0)	368.4 (12.8)	409.6 (73.0)	536.1 (98.8)	642.7 (34.9)	677.3 (121.8)

Chapter 6

Canopy Openness, Understory Light Environments, and Oak Regeneration

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Abstract

Understory light environments were evaluated in four mixed-oak forests in southern Ohio using hemispherical photography. Within each forest, plots were divided into nine treatment combinations based on three pretreatment fire categories and three Integrated Moisture Index (IMI) categories. For each of 108 photographs we determined the percentage of open sky, direct beam, and diffuse radiation; the latter two variables were combined to produce an estimate of the percentage of global radiation reaching the regeneration layer (1.5 m). Global light ranged from less than 1 to 23 percent and averaged 5.5 to 8.3 percent across treatment combinations; it did not differ significantly as a function of study area, treatment unit, or IMI. Xeric sites had a significantly greater percentage of open sky, but this influenced primarily the amount of diffuse radiation rather than direct beam radiation. Nearly 75 percent of the variance in global radiation could be predicted from open sky. The relationship between in situ light availability and IMI was evaluated with respect to oak regeneration in the seedling, pole, and sapling size classes. There was no strong relationship between the amount of ambient light or IMI and the amount of oak regeneration. Under ambient conditions in mature mixed oak forest, light and moisture may not be the primary determinants of establishment and early survival.

Introduction

Forest canopy structure is a complex and dynamic outcome of years of evolution and ecological interactions between vegetation and the environment (Norman and Campbell 1991). Canopy structure varies at a variety of spatial and temporal scales (Hutchison and Matt 1977). Variability in the overstory translates directly to altered microenvironments in the understory (Minckler et al. 1973; Vitousek and Denslow 1986), with the most obvious effects being changes in ground layer light environments. The quality and quantity of the light that reaches the forest floor are determined by ambient abiotic conditions, biological features, and disturbance regimes (Endler 1993).

The radiation environment within forests is primarily a function of simple sun-earth geometry, topography, canopy architecture, optical properties of the vegetation, and the ratio between direct and diffuse radiation (Ross 1981; Baldocchi et al. 1984). Abiotic conditions and site-quality factors including soil parent material, soil texture and structure, ion availability, and hydrology influence the distribution, abundance, and structure of overstory tree species within the forest (Martin 1975; Anderson and Vankat 1978; Muller 1982; McCarthy et al. 1984, 1987; Chapter 3). In turn, the constituent overstory species with their respective leaf morphologies, densities, reflectivity, and crown characteristics are the primary biological determinants of light quality and quantity reaching the forest floor (Endler 1993). Branchfalls, treefalls, defoliations, diebacks, and other disturbances in the canopy add to these biological features to create a unique canopy architecture (Chazdon and Pearcy 1991). In natural systems, this architecture often is spatially and temporally diverse, leading to heterogeneous understory light environments (Chazdon 1988).

Although considerable microenvironmental information is available for intensively managed agricultural and forest monocultures (Ross 1981), natural systems with their attendant heterogeneity have been less well studied. Among forest ecosystems, forest understories have been studied most intensively in tropical vegetation (Pearcy 1983; Chazdon and Fetcher 1984; Chazdon and Pearcy 1986) and coniferous vegetation (Reifsnyder et al. 1971; Tajchman 1972; Norman and Jarvis 1974, 1975; Sinclair and Knoerr 1982). Temperate deciduous forests have

been reasonably well studied (Anderson 1964 a,b; Miller 1969; Horn 1971; March and Skeen 1976; Hutchison and Matt 1977; Canham 1988; Chason et al. 1991), but data still are limited because certain vegetation types have been neglected or the scope of research was too narrow and/or the techniques or sensors used were inappropriate (Baldocchi et al. 1984). Few data are available for mixed-oak forests using modern techniques of data acquisition and analysis (Baldocchi et al. 1984; Chason et al. 1991). The quantification of understory light environments is critical if we are to correctly parameterize forest growth models, understand light effects on regeneration ecology, and elucidate forest ecosystem processes.

The importance of canopy heterogeneity to understory light environments and microclimate in natural mixed-species systems has been recognized for many years (Weaver and Clements 1938; Daubenmire 1947; Oosting 1948). Light measurements in the forest have become more accurate and precise in recent years due to technological advancements (Pearcy 1991). Yet, there are relatively few methods with which to determine the amount of light that reaches the forest floor (Smith and Somers 1991). The method used depends on the goals of the study, the level of precision and accuracy desired, spatial scale (centimeters, meters, hectares), temporal scale (seconds, hours, months, years), and amount of resources available (time and money).

Quantum light sensors are generally used for short experiments involving the response of individual plants to abrupt changes in the amount of light received, i.e., sunflecks (Chazdon 1988). Photochemical sensors such as photosensitive sepia paper are used to evaluate the total amount of light received at a point over several day periods but the ability to resolve smaller changes in light intensity is sacrificed (Friend 1961). Data-collection techniques that include the use of photography have been described as being objective, accurate, and rapid ways of analyzing vegetation (Bonham 1989). Hemispherical photography is useful for estimating openness in forest overstories in a variety of environments (Hill 1924; Evans and Coombe 1959; Anderson 1964 a,b; Lin et al. 1992; Rich et al. 1993; Robison and McCarthy 1999).

Digital image analysis has greatly enhanced the precision and accuracy of hemispherical photography in determining understory light environments and allows a detailed analysis of light penetration through forest canopies (Rich 1990; Canham et al. 1990; Rich et al. 1993; Canham and Burbank 1994). This technique is relatively inexpensive, easily transported, can be replicated consistently over many years, and is desirable for comparative studies (Robison and McCarthy 1999). Hemispherical photographs have been used to indirectly estimate the percentage of solar radiation reaching the point where the photo was taken. Data collected include percentages of open sky, diffuse, direct, and global solar radiation (Smith and Somers 1994). A single photograph can be used to estimate the percentage of full-sun seasonal radiation at a particular site (Pearcy 1991).

The purpose of our study was to examine the ground-layer light environment in four oak-hickory forests in southeastern Ohio using hemispherical photography, and to evaluate the relationship between in situ oak regeneration and ambient light environments. Also, this study will provide baseline data that will be useful in examining the effects of prescribed fires on light regimes.

Methods

Study Areas and Experimental Design

The study areas and experimental design are described in detail in Chapter 1. Here a brief overview is provided. The four 75-90 ha study areas are located in Vinton County (Arch Rock and Watch Rock) and Lawrence County (Young's Branch and Bluegrass Ridge). The study areas are within in the Southern Unglaciated Allegheny Plateau, which is characterized by high hills, sharp ridges, and narrow valleys. Sandstones and shales are principle bedrocks. Forests are oak-dominated and the current overstory originated in the late-1800s, after the cessation of clearcutting for the charcoal iron industry.

In each study area, three prescribed fire treatments were established, a control unit (CONT), an infrequent burn unit (INFR), and a frequent burn unit (FREQ). To account for variation in soil moisture and vegetation, a GIS-derived integrated moisture index (IMI) was applied across the dissected landscapes of the study areas (Chapter 3). From the calculated IMI scores, each 30 x 30 m pixel was assigned to one of three soil moisture classes: xeric, intermediate, or mesic. Thus to examine the effects of prescribed fire and account for environmental heterogeneity, a split-plot experimental design was established. The four study areas are replicate blocks, fire treatment units are whole plots, and IMI classes are subplots. The 50 x 25 m vegetation plots (N= 108 total) were established as pseudoreplicates in each IMI class within each fire treatment unit (Chapter 1).

Field and Laboratory Methods

All 108 permanent plots (25 by 50 m) were used for the canopy analysis. A hemispherical photograph was taken at the exact center of each plot with a 35mm camera (Nikon FG-20) equipped with a Sigma 8mm fisheye lens mounted on a tripod. The height of the tripod was adjusted so the plane of the film surface was 1.5 m above the ground.

The camera body was leveled to a zero zenith angle using a bidirectional bubble level attached to the flash mount. From this position, three photos were taken at three consecutive f-stop settings to ensure proper exposure and contrast. For each photo, a sighting rod was placed nearby the camera so it could be seen through the viewfinder. The plot's identification code, the orientation (azimuth) of the sighting rod relative to the center of the lens, and the numbers associated with the exposures taken and roll of film used were recorded for each plot.

Throughout July 1995, photos were taken early or late in the day or under overcast conditions to avoid the definition-reducing "hot spot" caused by the solar disk (Smith and Somers 1991; Canham and Burbank 1994). Color slide film (Ektachrome 200, Kodak, Inc.) was used to increase the resolution between blue sky, clouds, foliage, tree trunks, branches, etc.

Following development, individual slides were scanned via an Agfa Arcus Plus flatbed scanner. FotoLook (v. 2.07b) interface and image-editing software was set to capture and crop the images (2.3 cm^2) at a resolution of 1,000 DPI in RGB format. The images were scaled to 50 percent before capture to reduce the size of the digitized slides to approximately 2.3 megabytes. The scanned images were edited using Adobe Photoshop (v. 2.5 for Windows). The east and west edges of the circular images were marked with green and red dots, respectively, based on the placement of the sighting rod. This software also was used to correct occasional flaws in images due to inclusion of the solar disk. These images, including the green and red east-west headings, were saved as *.bmp (bitmap) files and stored on compact disk using a write-to-CD unit (Pinnacle 1000 RCD). The original slides were archived in protective plastic sleeves.

Data Analysis

The digitized images were analyzed by Windows-based GLI/C (v. 3.1), a computer program designed by Dr. Charles Canham of the Institute of Ecosystem Studies, Millbrook, NY. The program superimposes the sun's path across the photo as it would normally move across the sky. The program repeats this process for as many days as the user defines. The regional dates for average last spring frost and first fall frost were used as the representative growing season (April 29 - October 8; 163d). The orientation of the photo (east-west headings) were entered according to the green and red markings on the images. The latitude of each plot was included in the analysis to ensure proper azimuth angle for the solar pathway.

Percentages are calculated for: open sky, beam radiation, diffuse radiation, and global radiation. Open sky is the percentage of sky that is visible through openings in the canopy; beam radiation is the percentage of radiation transmitted directly through openings in the canopy; diffuse radiation is the percentage of diffuse radiation that penetrates canopy openings; and global radiation is the combined percentage of diffuse and direct beam total seasonal radiation. The latter variable is equivalent to the Gap Light Index described in Canham (1988) and is arguably the best overall cumulative measure of light availability in the understory.

The statistical model for this project was classified as a mixed-effects, split plot with the main plots arranged in a crossed-effects block design. Study area served as the block and was treated as a random effect. Fire treatment and IMI (main effects) were treated as fixed effects. All data were analyzed using SAS v. 6.11 (SAS Inst. 1990). Data for the four variables were evaluated using the PROC MIXED procedure (SAS Inst. 1996). The MIXED procedure is a generalization of the GLM procedure and provides for more flexibility in modeling mixed effects. However, because it employs a modified estimation scheme it does not directly provide sum of squares; rather, variance components are estimated via a method known as residual maximum likelihood (REML). The fixed effects are tested using Type-III estimable functions; a containment approximation is used for the denominator degrees of freedom. *A posteriori* comparisons of main effects were made following Bonferroni corrections of the p-values for the lsmean differences.

We also examined the relationship between the number of stems in the oak regeneration size classes vs. global radiation (%) using ordinary least-squares regression. These analyses were performed by the regression procedure of NCSS (Hintze 1995). To meet the assumptions of normality and homogeneity of residuals, data were $\log_{10}$ transformed as appropriate. Regression diagnostics (Belsley et al. 1980) were used to increase the quality of the fit. As a result, several points were omitted from the analysis because of undue leverage or influence. Seedling (ht < 30 cm) data (N = 1003 stems) were available for all 108 plots while pole (d.b.h. < 2.5 and ht >30 cm; N = 56) and sapling (d.b.h. 2.5 to 9.9 cm; N =7) data were available only for 54 plots. Because of the low sample size in the sapling data set, saplings and poles were combined for analysis. The regeneration sampling methods are described in Chapter 8.

Results

Analysis of variance (Table 1) indicated that neither the pretreatment identity (assigned burn regime) nor the IMI significantly affected global light levels (all $P > 0.05$). Global light averaged 5.5 to 8.3 percent across treatment units (Fig. 1). Global light can be decomposed into beam

radiation and diffuse radiation. Upon doing this, it became clear that direct beam radiation was not influenced by pretreatment units or IMI (all $P > 0.05$; Table 1). However, diffuse beam radiation differed significantly among pretreatment units ($P = 0.0556$; Table 1) and IMI ($P = 0.0209$; Table 1). These differences were driven largely by the increased diffuse light on xeric plots in the control and infrequent units (Fig. 1). Direct beam radiation averaged 6.1 to 9.7 percent vs. 4.7 to 7.5 percent for diffuse beam radiation. The amount of open sky (3.2 to 5.7 percent) showed a similar pattern with respect to the diffuse beam radiation, i.e., strong effects of treatment unit ($P = 0.0592$) and IMI ($P = 0.0041$; Table 1). There were no significant interactions between treatment units and IMI for any dependent variables (Table 1). Study area was treated as a random effect and was not tested in the mixed-model analysis. A separate GLM procedure indicated no significant differences among the four study areas (all $P > 0.10$).

To determine whether the percentage of open sky can be used to indirectly assess overall understory light conditions, we conducted a separate regression analysis of open sky vs. global radiation. The overall regression was highly significant ($P < 0.0001$), with a y-intercept indistinguishable ($P < 0.003$) from zero. The coefficient of determination ($R^2 = 0.636$) and power (1.000) were sufficiently high to conclude that the percentage of open sky is a reasonably good predictor of global radiation (Fig. 2).

Histograms were produced to summarize the amount of oak (*Quercus* spp.) regeneration in the 108 plots. Data were tallied at the genus level, so all species were combined for these analyses. Because pole and sapling data were available only for half of the plots, these data were scaled by a factor of two to make them comparable to the seedling data. Seedlings were found in all but two sample plots and occurred as >5 individuals per plot in 60 of the samples, the modal category (Fig. 3). The modal category for poles was one to two poles per plot. The modal category for saplings was zero (80 plots) with one to two stems in 28 plots. As expected, the data indicate a steady decline in abundance across size classes from seedlings to saplings (Fig. 3).

Regression analyses were conducted to evaluate the relationship between number of stems in a size class for each sample plot and the ambient global light percent for that plot (Fig. 4). The seedling class yielded a nonsignificant regression with very poor fit and weak power, as did the combined pole and sapling data (Fig. 4). There did not appear to be a relationship between light and ambient oak reproduction, at least under the range of ambient light environments encountered in these mature mixed oak forests.

Discussion

Hemispherical photography can provide an accurate measure of understory light conditions as there apparently is a strong relationship between photosynthetically active radiation (PAR) and canopy openness. Becker et al. (1989) and Rich et al. (1993) found excellent agreement between hemispherical canopy photographs and actual photosynthetic photon flux densities measured via sensors.

Using hemispherical photography, we determined that the average grand mean of global radiation (across all treatment combinations) was 6.6 percent. This value is considerably greater than those for relative transmittance measured in other North American temperate deciduous forests. Horn (1971) observed transmittance of 2.9 percent in a New Jersey

Table 1.—Analysis of variance for two-way randomized block design using unbalanced mixed-effects model; study areas treated as random effects and Integrated Moisture Index: treated as fixed effects.

Variable	Source	Num. dfdf	Den. dfdf	F	P
Open sky	Treatment	2	6	4.70	0.0592
	IMI	2	18	7.58	0.0041
	Trt * IMI	4	18	1.14	0.3714
Beam	Treatment	2	6	1.92	0.2264
	IMI	2	18	0.18	0.8381
	Trt * IMI	4	18	0.61	0.6599
Diffuse	Treatment	2	6	4.86	0.0556
	IMI	2	18	4.84	0.0209
	Trt * IMI	4	18	1.11	0.3814
Global	Treatment	2	6	2.77	0.1407
	IMI	2	18	0.74	0.4930
	Trt * IMI	4	18	0.75	0.5719

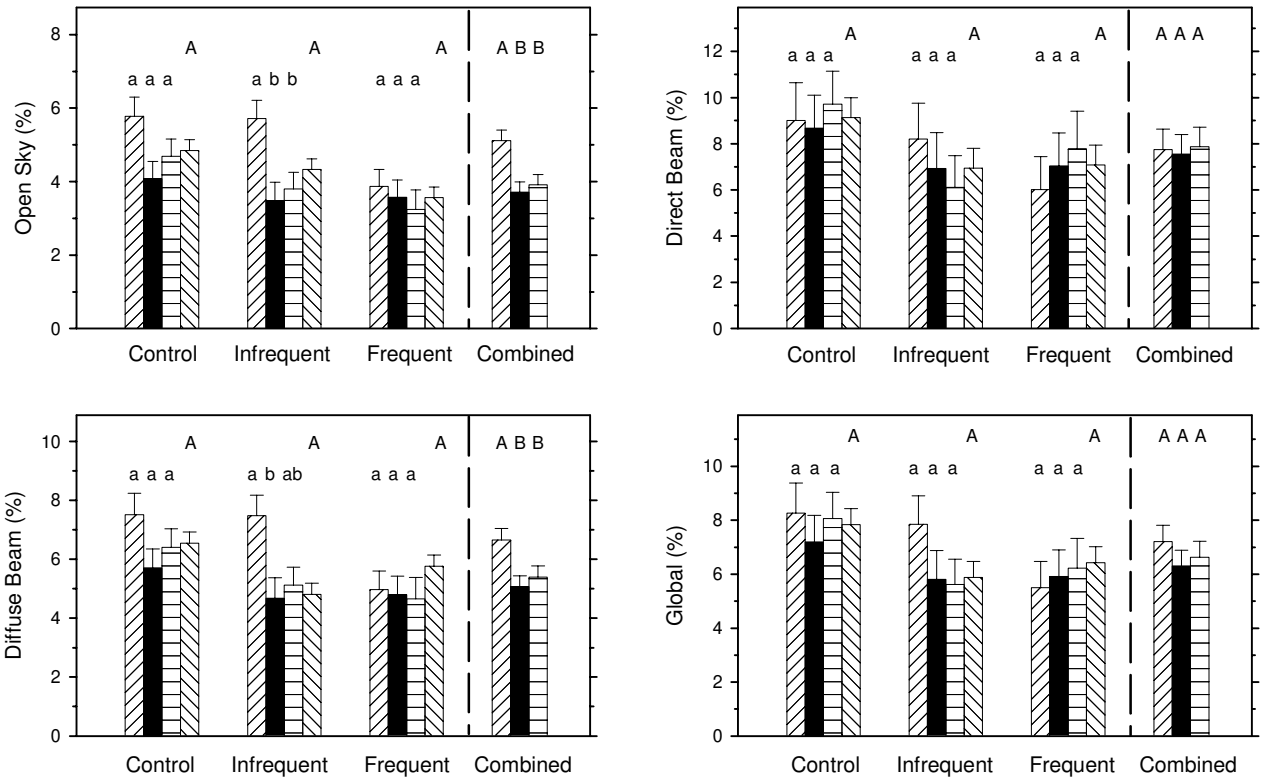

Figure 1.— Least squares means (±SE) for the four light environment variables (%): open sky, direct beam, diffuse beam, and total global radiation. Control, infrequent, and frequent refer to treatment designations. Fill colors designate the integrated moisture index (IMI) level: rising-right hatch = xeric, filled = intermediate, horizontal hatch = mesic, rising-left hatch is the overall mean for that burn regime. Data to the right of the dashed line within a panel are overall means for the IMI's. Letters are used to designate adjusted Bonferroni comparisons. Means with the same case letter within a line of a panel are not significantly different from each other ($P > 0.05$).

Piedmont forest, March and Skeen (1976) found that global radiation was about 3 percent beneath a Georgia hardwood-pine forest and Hutchison and Matt (1977) observed transmittance of 2.2 percent in 50-yr-old yellow-polar stands in Tennessee. Floyd et al. (1978) measured PAR above and below a mixed-oak forest during several phenological stages. They reported that 98 percent of incident PAR was attenuated by the forest canopy following foliar development. Baldocchi et al. (1984, 1986) recorded similar results (PAR below 3 percent) in an uneven-aged oak-hickory stand in Tennessee. In southwestern Wisconsin, Lorimer et al. (1994) recorded light levels as low as 1 percent in closed-canopy forests dominated by red and white oak.

The discrepancy between the light environment descriptions in these studies and our study likely is due to a variety of biotic (species) and abiotic (site quality) factors. For example, Canham and Burbank (1994) found that light transmittance was closely correlated with the degree of shade tolerance of the dominant species. Hemlock and beech stands provided less than 1 percent light transmission to the understory, maple stands allowed 2.4 to 4.4 percent, and stands dominated by red oak and ash allowed 5.7 and 6.2 percent, respectively. Thus, the data obtained from our mixed-oak stands might be explained largely by species composition and attending foliar spectral qualities. The discrepancy between our data and those from other mixed-oak stands (i.e., Baldocchi et al. 1984, 1986) probably can be attributed to the increased length of growing season, different solar path, and higher site qualities in southern Appalachian than in central Appalachian forests. Site quality affects growth, density, and crown closure in most hardwood stands (Daniel et al. 1979). As a result, light transmission to the forest floor is directly affected by stand density, leaf-area index, tree spacing, crown closure, and basal area (Reifsnyder and Lull 1965).

Interestingly, Canham and Burbank (1994) did not find significant differences in light transmittance as a function of height within the range of 1.0 to 7.5 m above ground in any forest type they studied. Thus, the available light to seedlings, poles, and saplings in any given area should be similar on average. Our data are consistent with this observation in that we found no relationship between global light and any regeneration size class of oak.

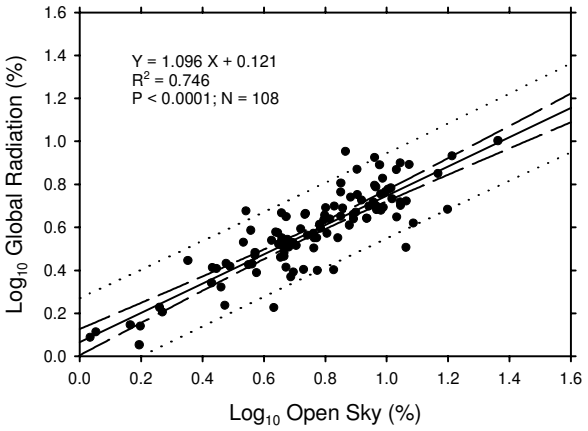

Figure 2.—Ordinary least-squares regression of open sky (percent) vs. total global radiation (percent). Data were $\log_{10}$ transformed to meet normality and homogeneity of variance assumptions. Solid line represents the best fit OLS line; dashed lines represent the upper and lower 95 percent confidence intervals, respectively; dotted lines represent the predication intervals. Approximately 75 percent of the global radiation can be predicted by open sky.

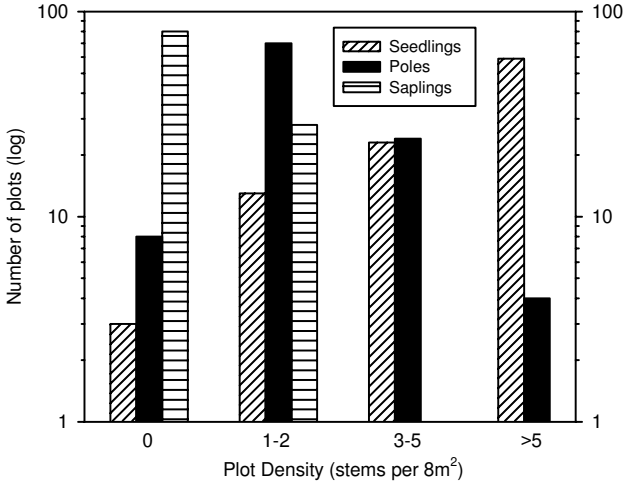

Figure 3.—Frequency histogram ($\log_{10}$ scale) for the distribution of seedlings (ht < 30 cm), poles (ht ³ 30 cm and d.b.h. < 2.5 cm), and saplings (d.b.h. 2.5-10.0 cm) in the 108 study plots.

Midstory interference via tall saplings is a potentially important factor in the development of oak seedlings beneath mature oak stands. Lorimer et al. (1994) removed saplings of maple, hornbeam, and basswood for 5 years in a Wisconsin forest to form a park-like area that might be representative of a system characterized by repeated light fires (Abrams 1988). They found an enormous release effect as oak seedlings were able to recruit and grow significantly better on experimental removal plots compared to control plots. Lorimer et al. (1994) recorded radiation as low as 1 percent beneath closed-canopy controls and as high as 7 to 9 percent on experimental removal plots. Their experimental removal plots were similar to our 6.6-percent light environments with undisturbed midstories. However, we did not observe increased oak abundance in any structural layer (seedlings, poles, saplings) at global light of 10 to 25 percent.

Phares (1971) found that oak is photosynthetically saturated at 30 to 50 percent of full sunlight; oak can maintain optimal height growth in sunlight as low as 8 percent (Loach 1967; Hodges and Gardiner 1994). These data suggest that the ambient light found in our study areas in southern Ohio should be adequate for oak regeneration and that light may not be the "limiting" factor for establishment and growth.

Oak has ecological and physiological properties that limit its ability to respond to changing light environments. Small oak seedlings have been reported as poor competitors across a range of disturbance regimes from small canopy gaps to large overstory disturbances (Beck 1970; Ehrenfeld 1980; McGee 1984). Plants generally respond to low resource levels by favoring the growth of the organ responsible for capturing the most limiting resource (Fitter 1986). High root:shoot ratios have long been known as adaptations to drought (Levitt 1972), and oaks and hickories are well known for their high root:shoot ratios (Kozlowski et al. 1991) and adaptations to drought (Abrams 1990). This suggests that the limiting resource may well be a below-ground resource (moisture or fertility) rather than an above-ground resource (light). The relationship between root:shoot ratio and drought tolerance has been demonstrated for both oak (Kolb et al. 1990) and hickory (McCarthy and Bailey 1994). Thus, these plants would be classified as moderate stress tolerators (sensu Grime 1979) and their ecological strength should be greatest where resource levels allow them to compete with less stress-tolerant species (Kolb et al. 1990). This has been a partial explanation for why oak regeneration increases as site productivity decreases (McGee 1979).

Long-term studies of solar radiation can be effectively studied through the use of hemispherical photography, but they are quite rare (Rich et al. 1993). This study provides baseline data from which to examine the long-term effects of prescribed fire on understory light regimes in mixed oak forests. Long-term environmental monitoring of light and soil conditions under an experimental burn regime may provide increased insight into how these effects ultimately influence oak regeneration.

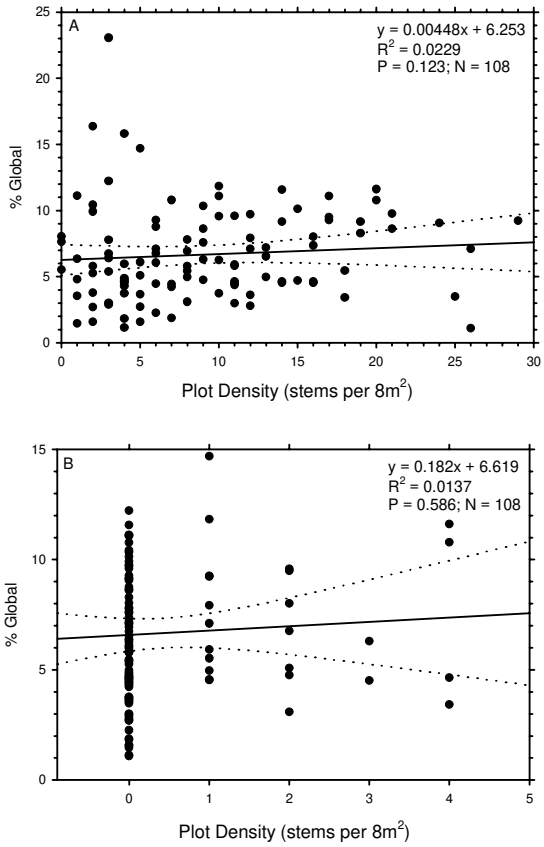

Figure 4.—Ordinary least-squares regression of number of stems vs. total global radiation (percent). Solid line represents the best fit OLS line, dashed lines represent the upper and lower 95 percent confidence intervals, respectively. (A) = seedlings; (B) = poles and saplings combined.

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Chapter 7

Understory Vegetation

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Abstract

This chapter documents patterns of species composition and diversity within the understory vegetation layer and provides a species list for the four study areas in southern Ohio. Within each of 108 plots, we recorded the frequency of all vascular plant species in sixteen 2-m^2 quadrats. We recorded 297 species, including 187 forbs (176 perennials, 9 annuals, 2 biennials), 44 graminoids, 34 shrubs and woody vines, and 32 trees. Only seven species were nonnatives and none of these were abundant. We also documented 12 state-listed species. Detrended correspondence analysis indicated that variation in species composition was primarily along a soil moisture-fertility gradient described by the Integrated Moisture Index. Additional variation in composition among the study areas was correlated with differences in soil texture. Species richness per plot (32-m^2 sampled) ranged from 23 to 106 and averaged 65.2; richness per quadrat averaged 16.7. All measures of species diversity were significantly higher on mesic than on xeric plots, primarily because forb richness was higher on mesic plots.

Introduction

In forested ecosystems, overstory trees largely control primary productivity as well as the cycling of water, nutrients, and gases. Yet the understory vegetation layer, composed of forbs, graminoids, shrubs, vines, and seedlings of tree species, accounts for most of the vascular plant diversity.

The composition of understory communities varies both spatially and temporally in response to resource gradients. Spatially, species are distributed across gradients of soil moisture and nutrient availability that result from variations in elevation, topography, soils, and disturbance history (Bray and Curtis 1957; Beals and Cope 1964; Siccama et al. 1970; Pregitzer and Barnes 1982). Temporally, plant species composition changes over long periods during secondary succession (Oosting 1942; Vankat 1991). Over shorter periods, the cover and abundance of herbaceous species vary annually in response to weather conditions (Rogers 1983) and throughout the growing season as different species emerge and reach maximum biomass at different times (Bratton 1976; Mahall and Bormann 1978; Goebel et al. 1999).

Within the Unglaciated Allegheny Plateau of southern Ohio are numerous "definitive" species that are found only in this region of the state (Silberhorn 1970). These species have centers of distribution in the Appalachian and Cumberland Mountains to the south and east (Thompson 1939; Silberhorn 1970). Across the region, plant distributions are related to differences in bedrock geology (Cusick and Silberhorn 1977).

At a more local scale, the dissected topography of the region produces microclimatic gradients of solar radiation, humidity, and soil moisture (Hutchins et al. 1976) that are strongly related to the distributional patterns of tree species (Muller 1982) and understory vegetation (Olivero and Hix 1998). The Integrated Moisture Index (IMI) used in our study predicts relative soil moisture across the landscape and stratifies vegetation plots into classes likely to be similar in species composition and ecological functioning (Chapter 3).

In this chapter we describe general characteristics of the flora found in the study areas and quantify vegetation-environment relationships. Specifically, we sought to determine how patterns of species composition and diversity vary among the three IMI classes (xeric, intermediate, and mesic). Also, as a component of the ecosystem management study, the results will provide baseline data for examining the long-term effects of prescribed fire on understory vegetation.

Methods

Study Areas and Experimental Design

The study areas and experimental design are described in detail in Chapter 1. Here a brief overview is provided. The four 75-90 ha study areas are located in Vinton County (Arch Rock and Watch Rock) and Lawrence County (Young's Branch and Bluegrass Ridge). The study areas are within in the Southern Unglaciated Allegheny Plateau, which is characterized by high hills, sharp ridges, and narrow valleys. Sandstones and shales are principle bedrocks. Forests are oak-dominated and the current overstory originated in the late-1800s, after the cessation of clearcutting for the charcoal iron industry.

In each study area, three prescribed fire treatments were established, a control unit (CONT), an infrequent burn unit (INFR), and a frequent burn unit (FREQ). To account for variation in soil moisture and vegetation, a GIS-derived integrated moisture index (IMI) was applied across the dissected landscapes of the study areas (Chapter 3). From the calculated IMI scores, each 30 x 30 m pixel was assigned to one of three soil moisture classes: xeric, intermediate, or mesic. Thus to examine the effects of prescribed fire and account for environmental heterogeneity, a split-plot experimental design was established. The four study areas are replicate blocks, fire treatment units are whole plots, and IMI classes are subplots. The 50 x 25 m vegetation plots (N= 108 total) were established as pseudoreplicates in each IMI class within each fire treatment unit (Chapter 1).

Vegetation sampling

To account for varying phenologies of herbaceous species, the understory vegetation was sampled in the spring (April 26 to June 14) and again in late summer (August 22 to September 14) of 1995. We used stratified random sampling on a 25- by 25-m portion of each vegetation plot. Four cross-slope transect lines were established at 5, 10, 15, and 20 m. Three 1- by 2-m quadrats were located randomly along each of the four transect lines using whole numbers (0-24) and placed above or below the line based on a random positive or negative designation. The quadrat locations were the same for spring and late summer. We also sampled an additional permanent quadrat at the midpoint of each line for a total of sixteen 1- by 2-m quadrats per plot.

To accommodate analyses of common and less frequent species, the 1- by 2-m quadrats were nested into three sections of 0.25, 1.0, and 2.0-m^2. For each species, its presence was recorded as first occurring in one of these sections. Here we report data only from the entire 2-m^2 quadrats. For tree species, presence was recorded in four size classes: less than 30 cm tall, 30 cm tall to 2.99 cm in diameter at breast height (d.b.h.), 3.0 to 9.9 cm d.b.h., and 10 or more cm d.b.h.

In addition to the quadrat sampling, species that were listed as threatened and endangered (T&E) in Ohio by the Ohio Department of Natural Resources were noted in the plots. Also, in 1994 and 1995, rare plant surveys were conducted by walking through each study area. The locations of T&E species were submitted to the Ohio Natural Heritage Database (Ohio Department of Natural Resources, Division of Natural Areas and Preserves, Columbus, OH).

Data analysis

For each species, the total frequency per plot was determined as the maximum frequency recorded in either the spring or late summer sampling period. For tree species, the data presented include all four size classes but more than 85 percent of the trees tallied were in the smallest (< 30 cm) class.

Species richness was calculated for each plot by summing the total number of unique species in the 16 quadrats. Life form richness was then calculated for each plot by summing the total number of unique species in each life form category. Average species richness per quadrat was calculated from the cumulative frequency of each species divided by 16 quadrats. We used PC-ORD, ver. 3.0 for Windows, (McCune and Mefford 1997) to calculate species diversity (Shannon Index) and evenness for each plot.

To test for significant pretreatment effects of IMI and treatment units on richness and diversity, a mixed-model analysis of variance (SAS 6.12 for Windows; PROC MIXED, ML option) with maximum likelihood estimation was used (Littell et al. 1996). Study areas were treated as random effects and IMI and treatment units as fixed effects. We used least-squares means to test for significant differences among the IMI classes and treatment units. See Chapter 1 for a description of the statistical model used in this study.

We used detrended correspondence analysis (DCA) to describe patterns of species compositional change along environmental gradients (PC-ORD). The input data was a matrix of species' frequencies in the 108 plots. We used Pearson correlation analysis to quantify the relationship between DCA plot scores and environmental data from each plot. For detailed information on the environmental variables used in the analysis, see Chapters 3 (IMI), 5 (soils), 6 (light availability), and 9 (overstory).

Table 1.--Mean frequency for each common species per IMI class (XER = Xeric; INT = Intermediate; MES = Mesic). Common species are defined as occurring at >10% frequency in one or more IMI classes. N = 33 xeric, 37 intermediate, and 38 mesic plots. Nomenclature is from Gleason and Cronquist (1991).

SPECIES	ABB.	XER	INT	MES	SPECIES	ABB.	XER	INT	MES
Acer rubrum	Acru	76.3	66.4	57.8	*Lindera benzoin*	Libe	1.7	15.6	28.3
Acer saccharum	Acsa	4.8	22.5	30.7	*Liriodendron tulipifera*	Litu	14.3	30.9	33.3
Adiantum pedatum	Adpe	0.0	1.6	10.6	*Monarda fistulosa*	Mofi	0.7	2.0	10.1
Amelanchier arborea	Amar	23.3	6.6	7.3	*Nyssa sylvatica*	Nysy	21.5	13.8	20.0
Amphicarpaea bracteata	Ambr	18.8	21.4	17.2	*Osmorhiza spp.*	Ossp	1.5	7.1	17.9
Anemonella thalictroides	Anth	2.9	15.0	55.4	*Ostrya virginiana*	Osvi	11.6	8.2	3.0
Arisaema triphyllum	Artr	1.5	16.8	32.8	*Panicum boscii*	Pabo	20.2	15.5	3.1
Aristolochia serpentaria	Arse	7.0	11.8	11.1	*Panicum dichotomum*	Padi	11.9	3.5	0.9
Asarum canadense	Asca	0.0	5.4	32.1	*Parthenocissus quinquifolius*	Parqu	23.9	49.8	43.2
Aster divaricatus	Asdi	1.7	10.0	24.0	*Pilea pumila*	Pipu	0.2	6.1	12.8
Botrychium virginianum	Bovi	1.7	13.7	11.3	*Polystichum acrosticoides*	Poac	1.5	20.2	37.0
Brachyelytrum erectum	Brer	6.4	20.6	22.2	*Polygonatum biflorum*	Pobi	23.2	15.6	6.1
Carex digitalis	Cadi	5.3	9.9	9.5	*Potentilla canadensis*	Poca	16.4	18.4	9.7
Carex gracilescens	Cagrc	4.0	11.8	15.5	*Poa cuspidata*	Pocu	13.4	15.3	17.0
Carex wildenovii	Cawi	26.3	11.0	1.9	*Podophyllum peltatum*	Podpe	2.9	10.9	14.4
Carpinus caroliniana	Caca	0.4	4.9	12.3	*Prunus serotina*	Prse	11.4	12.2	7.1
Carya cordiformis	Carco	3.1	7.2	10.8	*Quercus alba*	Qual	36.8	22.9	15.8
Carya glabra	Cargl	19.3	14.8	11.6	*Quercus coccinea*	Quco	11.2	3.9	0.7
Cercis canadensis	Ceca	14.9	24.3	9.0	*Quercus prinus*	Qupr	28.7	8.4	3.3
Chimaphila maculata	Chma	9.9	3.8	1.2	*Quercus rubra*	Quru	11.2	11.2	10.4
Cimicifuga racemosa	Cira	0.2	12.2	30.7	*Quercus velutina*	Quve	25.4	11.7	4.7
Circaea lutetiana	Ciqu	1.5	7.1	17.9	*Rosa carolina*	Roca	23.5	11.7	5.7
Claytonia virginiana	Clavi	0.7	4.6	10.8	*Rubus spp.*	Rusp	20.2	26.5	15.1
Cornus florida	Cofl	44.1	37.3	29.3	*Sassafras albidum*	Saal	66.7	30.3	13.2
Crataegus spp.	Crsp	13.4	10.2	9.4	*Sanguinaria canadensis*	Saca	0.0	2.3	13.4
Cunila oreganoides	Cuor	12.1	1.2	0.0	*Sanicula spp.*	Sasp	8.5	17.6	14.2
Danthonia spicata	Dasp	10.8	1.0	0.0	*Scutellaria spp.*	Scsp	2.6	8.7	23.1
Dentaria laciniata	Dela	2.6	19.7	20.0	*Smilacinia racemosa*	Smra	19.5	40.1	34.5
Desmodium glutinosum	Degl	4.4	15.1	14.1	*Smilax glauca*	Smgl	40.6	31.7	16.8
Desmodium nudiflorum	Denu	41.0	53.3	37.5	*Smilax rotundifolia*	Smro	59.4	36.5	27.3
Dioscorea quaternata	Diqu	2.8	12.0	21.9	*Solidago caesia*	Soca	9.6	15.1	10.6
Eupatorium rugosum	Euru	3.9	14.3	20.8	*Thelypteris hexagonoptera*	Thhe	0.2	2.5	11.8
Fagus grandifolia	Fagr	10.1	10.2	17.4	*Tiarella cordifolia*	Tico	0.0	2.3	34.7
Fraxinus americana	Fram	22.6	45.7	34.9	*Toxicodendron radicans*	Tora	10.3	16.9	15.1
Galium aparine	Gaap	3.1	11.8	16.3	*Trillium grandiflorum*	Trgr	0.0	7.9	45.1
Galium circazans	Gaci	17.5	27.1	29.5	*Ulmus rubra*	Ulru	5.7	27.6	25.9
Galium concinnum	Gaco	0.0	5.8	11.3	*Uvularia perfoliata*	Uvpe	11.2	50.3	52.1
Galium triflorum	Gatr	8.5	35.4	36.3	*Vaccinium palidum*	Vapa	51.7	10.2	1.2
Geranium maculatum	Gema	4.4	36.3	62.3	*Vaccinium stamineum*	Vast	13.4	5.3	0.7
Hamamelis virginiana	Hamvi	2.0	6.1	11.5	*Viburnum acerifolium*	Viac	10.1	29.8	34.4
Helianthus divaricatus	Hedi	10.8	4.6	0.7	*Viola spp.*	Viosp	15.8	34.4	37.7

Results

We recorded 297 species distributed in 83 families and 198 genera (Appendix). The most species-rich families were Asteraceae (29 species), Cyperaceae (23), and Poaceae (17); the most species-rich genera were *Carex* (21 species) and *Aster* (10). The species were distributed as 187 forbs (176 perennials, 9 annuals, 2 biennials), 42 graminoids, 34 shrubs and woody vines, and 32 trees. Only seven nonnative species were recorded; the most frequent was *Rosa multiflora*, which was found in less than 1 percent of the quadrats.

Most species were relatively uncommon, with an average frequency of less than 10 percent for all three IMI classes (Appendix). There were 86 common species, defined as having an average frequency of 10 percent or more in at least one IMI class (Table 1). The most frequent species (averaging more than 40 percent) on xeric plots were woody and included *Acer rubrum*, *Sassafras albidum*, *Smilax rotundifolia*, *Vaccinium palidum*, *Cornus florida*, and *Smilax glauca*; *Desmodium nudiflorum*, a forb, was also very frequent. On mesic plots, the most frequent species included four forbs, *Geranium maculatum*, *Uvularia perfoliata*, *Anemonella thalictroides*, and *Trillium grandiflorum*, and two

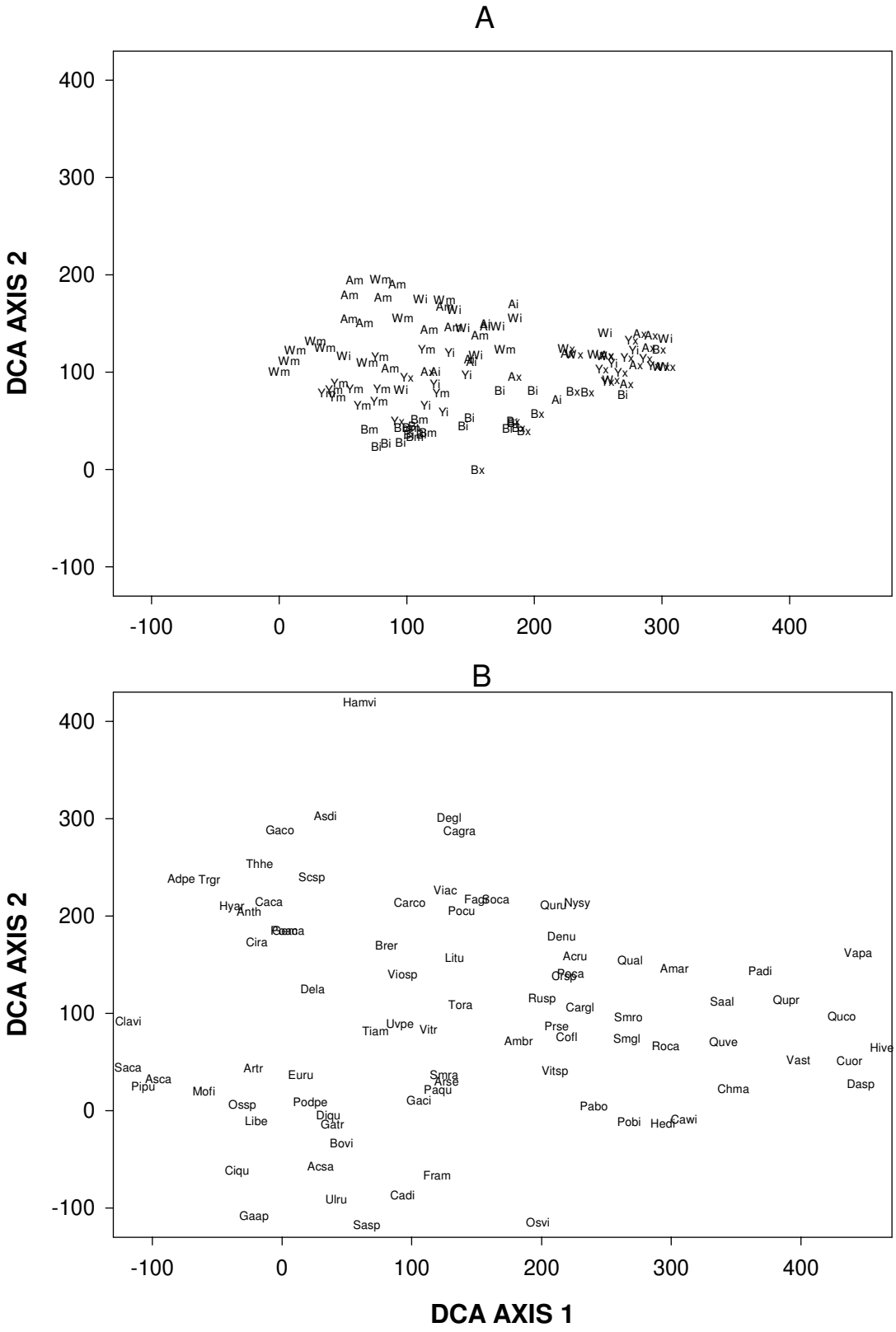

Figure 1.—Detrended correspondence analysis of the 108 vegetation plots. The input data for each plot was the frequency of each species recorded in 16 2 m^2 quadrats within a 25 X 25 m area. A. Each vegetation plot is represented by two letters denoting the study area (A = Arch Rock, B = Bluegrass Ridge, W = Watch Rock, and Y = Young's Branch) and IMI class (x = xeric, I = intermediate, and m = mesic). B. Each common species, defined as averaging >10% frequency at least one IMI class, is represented by a unique 4 or 5 letter code, based on the genus and species. The species codes are listed in Table 1.

Table 2.—Eigenvalues for the DCA axes and correlation coefficients (Pearson) for the environmental variables and the plot scores calculated in DCA. Only correlations significant at p<0.05 are listed.

Variable	Axis 1	Axis 2	Axis 3
IMI	-0.754	0.304	ns
NO_3	-0.694	ns	ns
pH	-0.626	-0.385	ns
NH_4	-0.587	ns	0.267
PO_4	-0.329	-0.448	-0.244
Light	0.194	ns	ns
Tree basal area	ns	ns	ns
Stand age	ns	ns	ns
Clay (%)	ns	-0.486	ns
Sand (%)	ns	-0.630	ns
Silt (%)	ns	0.606	ns
Eigenvalue	0.374	0.151	0.084

woody species, *Acer rubrum* and *Parthenocissus quinquifolius*. The most frequent species on intermediate plots were *Acer rubrum*, *Desmodium nudiflorum*, *Uvularia perfoliata*, *Parhtenocissus quinquifolius*, *Fraxinus americana*, and *Smilacina racemosa* (Table 1).

Detrended correspondence analysis

DCA indicated that plots were separated primarily along the moisture gradient predicted by the IMI classes. Mesic plots generally had low axis 1 scores and xeric plots had high axis 1 scores (Fig. 1a). The eigenvalues for axis 1 and 2 were 0.374 and 0.151, respectively (Table 2). Axis 1 plot scores were most strongly correlated with IMI (-0.754), NO_3^- (-0.694), pH (-0.626), and NH_4^+ (-0.587), indicating a compositional gradient also related to decreasing nutrient availability along axis 1 (Table 2).

Common species associated with the xeric sites included six woody species, *Vaccinium palidum*, *V. stamineum*, *Quercus coccinea*, *Q. prinus*, *Q. velutina*, *Sassafras albidum*, three forbs, *Hieraceum venosum*, *Cunila oreganoides*, *Chimaphilia maculata*, and two grasses, *Danthonia spicata* and *Panicum dichotomum* (Fig. 1b). Except for *Acer saccharum*, all of the species associated with the mesic plots were forbs, and included *Sanguinaria canadendsis, Claytonia virginiana, Pilea pumila, Adiantum pedatum, Monarda fistulosa*, and *Trillium grandiflorum*.

Many of the most frequent species were common in all IMI classes, and had intermediate axis 1 scores. Among these were *Rubus spp., Desmodium nudiflorum, Acer rubrum, Cornus florida*, and *Vitis spp*., which were found toward the xeric portion of axis 1, while *Viburnum acerifolium, Uvularia perfoliata, Smilacina racemosa, Parthenocissus quinquifolius, Galium circazans*, and *Fraxinus americana* were found toward the mesic portion of axis 1 (Fig. 1b).

Axis 2 indicated additional compositional variation among the four study areas (Fig. 1a). Although plots were not strongly separated by study area, BR plots had low axis 2 scores, WR and AR plots had high axis 2 scores, and YB plots were intermediate. For axis 2, the compositional variation among the study areas was primarily in the intermediate and mesic plots. Axis 2 plot scores were most strongly correlated to percent sand (-0.630), percent silt (0.606), and percent clay (-0.486) (Table 2).

Species associated with the AR and WR mesic plots included *Hammamelis virginiana, Aster divaricatus, Desmodium glutinosum, Galium concinnum,* and *Carex gracilescens*. Species associated with the mesic plots at BR included *Ostrya virginiana, Sanicula spp., Galium aparine, Ulmus rubra, Carex digitalis, Fraxinus americana, Circaea quadrisulcata*, and *Acer saccharum*.

Species richness and diversity

Species richness per plot ranged from 23 to 106 and averaged 65.2. Mean richness per quadrat (2-m^2) ranged from 6 to 30 and averaged 16.7. For 13 different measures of richness and diversity, there were no significant pretreatment differences among the fire treatment units (Tables 3-4). Also, there were no significant IMI x treatment interaction effects for any richness or diversity measure.

By contrast, all measures of total richness and diversity were significantly different among the IMI classes. Species richness was significantly greater on intermediate and mesic plots than on xeric plots, both at the scale of plot ($F = 10.34$, $p = 0.001$) and quadrat ($F = 11.32$, $p = 0.002$) (Table 3). Species evenness on mesic plots was significantly greater than on xeric plots ($F = 5.04$, $p = 0.02$). Species diversity also was significantly higher on intermediate and mesic than on xeric plots ($F = 9.59$, $p = 0.002$).

Among the four major life forms, forbs had the highest species richness, averaging 31.9 species per plot and 8.1 species per quadrat. There were significant differences in forb richness among IMI classes, both at the plot ($F = 23.21$, $p = 0.0001$) and quadrat ($F = 26.94$, $p = 0.0001$) scale of measurement; forb richness was significantly greater on mesic than on intermediate plots, which were significantly more rich than the xeric plots (Table 4). There were no significant IMI effects on the richness of tree species, graminoids, shrubs, or woody vines (Table 4).

Threatened and endangered (T&E) species survey

Twelve state-listed T&E species were identified in the four study areas (Table 5). Arch Rock had the most species

Table 3.—Mean values for measures of total species richness per plot from ANOVA testing for effects of IMI and treatment unit; no significant IMI*unit interactions; significant differences among least squares means represented by different letters for treatment units (a,b,c) and IMI classes (d,e,f).

	Treatment unit			
IMI class	Control	Infrequent	Frequent	Mean
	Species richness/plot			
Xeric	51.0	54.4	61.6	55.7_{d}
Intermediate	58.7	72.2	69.4	66.8_{e}
Mesic	71.4	74.8	69.2	71.8_{e}
Mean	60.4_{a}	67.1_{a}	66.7_{a}	
	Species richness/quadrat			
Xeric	11.8	12.7	16.3	13.6_{d}
Intermediate.	14.9	17.8	17.8	16.8_{e}
Mesic	19.1	20.0	17.9	19.0_{e}
Mean	15.3_{a}	16.8_{a}	17.4_{a}	
	Evenness/plot			
Xeric	0.90	0.912	0.909	0.910_{d}
Intermediate.	0.916	0.916	0.919	0.917_{de}
Mesic	0.926	0.922	0.925	0.924_{e}
Mean	0.917_{a}	0.917_{a}	0.917_{a}	
	Species diversity/plot			
Xeric	3.56	3.63	3.69	3.63_{d}
Intermediate.	3.70	3.91	3.88	3.83_{e}
Mesic	3.95	3.97	3.92	3.95_{e}
Mean	3.74_{a}	3.84_{a}	3.83_{a}	

(eight) and YB the fewest (two). Two species, *Calamagrostis porteri* subsp. *insperata,* and *Gentiana villosa* were listed as endangered, the highest conservation category in Ohio. Both were found in relatively xeric areas, i.e., on ridgetops, or south- or west-facing slopes.

Discussion

The 297 species recorded in this study represent approximately 15 percent of the more than 2,000 species known from southeastern Ohio (Cusick and Silberhorn 1977). A flora of the Vinton Furnace Experimental Forest (VFEF) documented 536 species for the 485-ha area (Hall 1958). Even though our sampling at AR and WR (in and adjacent to the VFEF) was confined to upland closed-canopy forests and covered less than 0.03 percent (0.173 ha) of the area surveyed by Hall, we recorded 260 species at these sites.

Surprisingly, we recorded only seven exotic species, and none of these were abundant. Ecosystems that experience relatively mild and/or infrequent anthropogenic disturbance generally are less susceptible to invasion by exotic species (Rejmanek 1989). In the 1800s, our study areas were disturbed by clearcutting and likely by fire and grazing, while selective harvesting likely occurred in the 1900s (Chapter 2). Although Hall (1958) recorded 45 exotic species in his survey of the VFEF, nearly all were restricted to disturbed areas such as roadsides, lawns associated with buildings, open bottomlands, and recently harvested stands. Our results indicate that despite a presumably large pool of exotic species in the area, few can establish or persist in upland mature forests.

Relatively few T&E species were recorded in the sampling and surveying, probably because our study areas are fairly typical of large portions of southeastern Ohio. The Pennsylvanian sandstone underlying the study areas is the most common bedrock type in the Unglaciated Allegheny Plateau of southern Ohio (Cusick and Silberhorn 1977). By contrast, the uncommon outcrops of Silurian limestones and dolomites located south and west of the study areas in Adams County contain numerous T&E species (Cusick and Silberhorn 1977).

In landscapes with significant topographic variation, plant species composition often is most strongly related to gradients of aspect (Lieffers and Larkin-Lieffers 1987; Olivero and Hix 1998), slope position (Bridge and Johnson 2000), or an integration of both (Allen and Peet 1990), that result in variation in microclimate and soil moisture. Similarly, we found that understory composition was most strongly related to the IMI, which incorporates aspect (hillshade index, 40 percent), slope position (cumulative flow of water downslope, 30 percent), soil water-holding capacity (20 percent) and curvature (10 percent) (Chapter 3). Species composition also was strongly related to soil NO_3^-, pH, and NH_4^+, which varied directly with the IMI (Chapter 5). Moisture-fertility gradients control patterns of species composition in many ecosystems (e.g., Neave et al. 1995; Smith 1995; Bridge and Johnson 2000).

More than half of the common species associated with the xeric plots were woody, and included several species of *Quercus*, *Vaccinium*, and *Smilax* (Fig. 1b). *Quercus spp*. and *Vaccinium spp*. have morphological and physiological traits that infer a degree of resistance to drought (Parker and Pallardy 1988; Matlack et al. 1993; Pallardy and Rhoads 1993). Despite the greater overall richness of forbs in the regional species pool, relatively few forb species establish and persist on xeric, nutrient-poor slopes. In sharp contrast, more than 75 percent of the common species associated with the mesic plots were forbs (Fig. 1b). Similar patterns of life form distribution have been quantified by Mabry et al. (2000),

Table 4.—Mean values for species richness of life forms from ANOVA testing for the effects of IMI and treatment unit; significant differences among least squares means are represented by different letters for treatment units (a,b,c) and IMI classes (d,e,f).

	Treatment Unit			
IMI class	Control	Infrequent	Frequent	Mean
		Forb richness		
Xeric	17.7	20.8	26.9	21.8_{d}
Intermediate	25.7	37.1	34.8	32.6_{e}
Mesic	40.7	41.9	37.0	40.0_{f}
Mean	28.0_{a}	33.3_{a}	32.9_{a}	
		Forb richness/Quadrat		
Xeric	3.3	3.8	6.0	4.4_{d}*
Intermediate	5.9	8.6	8.7	7.7_{e}
Mesic	11.8	12.3	10.1	11.4_{f}
Mean	7.0_{a}	8.2_{a}	8.3_{a}	
		Graminoid richness/Plot		
Xeric	6.6	7.3	9.0	7.6_{d}
Intermediate	6.8	8.4	8.4	7.9_{d}
Mesic	5.2	7.3	5.9	6.1_{d}
Mean	6.2_{a}	7.7_{a}	7.8_{a}	
		Graminoid richness/Quadrat		
Xeric	1.0	1.3	1.8	1.4_{d}
Intermediate	1.3	1.9	1.7	1.5_{d}
Mesic	1.0	1.4	1.2	1.2_{d}
Mean	1.1_{a}	1.5_{a}	1.6_{a}	
		Shrub and vine richness/Plot		
Xeric	9.6	10.5	9.7	9.9_{d}
Intermediate	9.7	11.5	10.9	10.7_{d}
Mesic	11.1	10.7	11.1	10.9_{d}
Mean	10.1_{a}	10.9_{a}	10.5_{a}	
		Shrub and vine richness/Quadrat		
Xeric	2.7	3.0	3.2	3.0_{d}
Intermediate	2.9	2.9	2.9	2.9_{d}
Mesic	2.8	2.6	2.5	2.7_{d}
Mean	2.8_{a}	2.9_{a}	2.9_{a}	
		Tree richness/Plot		
Xeric	17.1	15.9	16.1	16.3_{d}
Intermediate	16.7	15.1	15.2	15.7_{d}
Mesic	14.5	14.9	14.9	14.8_{d}
Mean	16.1_{a}	15.3_{a}	15.4_{a}	
		Tree richness/Quadrat		
Xeric	4.6	4.6	5.2	4.8_{d}
Intermediate	4.7	4.3	4.6	4.5_{d}
Mesic	3.9	3.8	4.1	3.9_{d}
Mean	4.4_{a}	4.6_{a}	4.2_{a}	

*Overall F test significant.

who reported traits associated with xeric habitat include woody roots and the ability to sprout while traits associated with mesic areas included low capacities for vegetative spread and root storage.

Species composition also varied among the four study areas, though most of that variation occurred among the intermediate and mesic plots (Fig. 1a). Boerner et al. (Chapter 5) also found that the xeric plots were relatively similar among the study areas. However, the mesic plots at BR had more Ca and Mg and had higher percentages of clay and sand than the AR and WR mesic plots. These results suggest that regional differences in bedrock geology caused additional variation in species composition, particularly the interbedded limestone associated with the lower slopes at BR.

Despite some variation in overstory composition, tree basal area and light availability generally were similar across the landscape (Chapters 6 and 9). Overstory structure variables were not strong correlates with plant composition probably because of the spatial homogeneity of light availability. In ecosystems with spatially heterogeneous structure (e.g., oak savannas), the distribution of species is strongly related to light availability (Leach and Givnish 1999).

Plant species diversity often is greatest in habitats with intermediate resource levels (Tilman 1982). By contrast, we found that diversity was greatest in mesic plots, which also had the greatest nutrient availability. Findings similar to ours have been reported for upland forests (Glenn-Lewin 1975; Huebner and Randolph 1995; Jenkins and Parker 1999). However, we did not sample the entire resource gradient for these study areas, because plots were not located in ravines and bottomlands. In a regional analysis in Illinois, tree species diversity was higher in upland mesic sites than in lowland wet-mesic sites (Adams and Anderson 1980).

For large-scale, long-term ecosystem studies, it is critical to quantify initial landscape patterns of structure, composition, and function (Stohlgren et al. 1995). The IMI was designed to map potential moisture conditions across a complex landscape. The IMI was positively correlated with soil nitrogen and pH, and thus also captured some of the variation in soil fertility. For studies of understory vegetation, our results indicate that the IMI is a useful tool.

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Table 5.—State-listed threatened and endangered plant species recorded in 1994 and 1995 on surveys of each study area (P=potentially state threatened, T=state threatened, E=state endangered).

Species	Ohio Status	Study area	Regional habitat description[a]
Asclepias amplexicaulis	P	AR	Dry fields, prairies and open woods
Calamagrostis insperata	E	AR,WR	Dry rocky woods
Carex abscondita	P	BR	Moist to wet woods
Carex juniperorum	T	BR	Open woodlands with limestone bedrock
Cirsium carolinianum	T	AR	Dry woods
Clitoria mariana	P	AR,WR	Dry upland woods and barrens
Cyprepedium calceoulus var. pubescens	P	AR,WR,YB	Mesic woods and ravines
Desmodium pauciflorum	P	YB,BR	Moist woods
Gentiana villosa	E	BR	Dry woods and prairies
Malaxis unifolia	P	AR	Oak woods
Rhododendron periclymenoides	T	YB	Moist or dry woods and bogs
Scutellaria serrata	P	AR	Mesic woods and ravines

[a]From Cusick and Silberhorn (1977), Gleason and Cronquist (1991), and Catling et al. (1993).

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Appendix. Mean frequencies/plot for vascular plant species recorded in 1995 (F=forb, G=graminoid, SV=shrub/woody vine, T = tree).

SPECIES	Life Form	IMI class			Study Area			
		Xeric	Intermediate	Mesic	Watch Rock	Arch Rock	Young's Branch	Bluegrass Ridge
		Percent			Percent			
Division Polypodiopyta (Ferns)								
Ophioglossaceae								
Botrychium dissectum	F	0.0	0.5	0.0	0.0	0.0	0.0	0.7
Botrychium virginianum	F	3.6	10.3	12.7	5.8	3.2	12.5	14.8
Osmundaceae								
Osmunda cinnamomea	F	0.0	0.0	2.0	0.0	2.8	0.0	0.0
Osmunda claytonia	F	0.0	2.2	6.3	4.6	5.1	0.9	1.2
Adiantaceae								
Adiantum pedatum	F	0.0	0.5	11.2	4.9	4.9	6.7	0.0
Aspleniaceae								
Asplenium platyneuron	F	0.4	1.2	0.5	0.5	0.9	0.2	1.2
Athyrium filix-femina	F	0.0	0.7	2.0	1.4	1.9	0.5	0.0
Athyrium thelpterioides	F	0.0	0.0	1.6	2.1	0.2	0.0	0.0
Cystopteris protrusa	F	0.0	0.0	0.2	0.2	0.0	0.0	0.0
Cystopteris spp.	F	0.0	0.0	1.5	2.1	0.0	0.0	0.0
Dryopteris spinulosa	F	0.0	0.2	0.0	0.2	0.0	0.0	0.0
Polystichum acrosticoides	F	3.6	18.2	35.7	23.6	23.6	20.4	12.0
Thelypteris hexagonoptera	F	0.2	2.0	11.7	6.5	6.0	6.7	0.2
Thelypteris noveboracensis	F	0.0	0.7	9.4	3.5	9.5	1.2	0.0
Onoclea sensibilis	F	0.0	0.0	1.8	2.3	0.2	0.0	0.0
Division Pinophyta (Gymnosperms)								
Pinaceae								
Pinus spp.	T	0.2	0.3	0.0	0.0	0.0	0.5	0.2
Division Magnoliophyta (Flowering Plants)								
Magnoliaceae								
Liriodendron tulipifera	T	13.3	30.2	34.4	31.3	22	30.6	22.2
Lauraceae								
Lindera benzoin	SV	6.4	10.0	28.6	8.8	9.7	31.3	12.0
Sassafras albidum	T	63.1	35.8	12.8	27.5	40.7	38.0	38.0
Aristolociaceae								
Aristolochia serpentaria	F	7.4	11.8	10.7	10.0	8.1	6.5	15.7
Asarum canadense	F	2.1	2.0	32.1	15.3	4.6	30.6	0.0
Ranunculaceae								
Anemonella thalictroides	F	4.7	12.0	54.3	27.8	31.5	30.8	8.6
Cimicifuga racemosa	F	2.7	9.3	30.1	18.3	14.4	20.8	4.9
Clematis virginiana	SV	0.2	0.3	0.0	0.0	0.2	0.0	0.5
Delphinium tricorne	F	0.0	0.2	0.0	0.0	0.0	0.0	0.2
Hepatica americana	F	0.4	1.4	8.7	4.9	9.3	0.0	0.5
Hydrastis canadensis	F	0.0	3.5	3.1	1.4	0.7	0.7	6.5
Ranunculus allegheniensis	F	0.6	0.2	1.8	2.8	0.7	0.0	0.0
Ranunculus hispida	F	0.6	1.9	0.2	0.5	1.4	0.0	1.6
Ranunculus recurvatus	F	0.6	2.9	2.3	0.0	0.2	1.9	5.8
Thalictrum dioicum	F	0.0	0.3	0.0	0.2	0.2	0.0	0.0
Thalictrum revolutum	F	0.0	0.2	0.0	0.0	0.0	0.0	0.2
Berberidaceae								
Caulophyllum thalictroides	F	0.0	0.7	2.3	1.4	0.2	2.5	0.0
Jeffersonia diphylla	F	0.0	1.7	0.0	0.0	0.0	0.0	2.3
Podophyllum peltatum	F	4.0	9.5	14.5	10.9	5.6	11.3	10.4

Appendix cont.

SPECIES	Life Form	IMI class			Study Area			
		Xeric	Intermediate	Mesic	Watch Rock	Arch Rock	Young's Branch	Bluegrass Ridge
		Percent			Percent			
Menispermaceae								
Menispermum canadense	SV	0.4	0.3	0.5	0.5	0.7	0.5	0.0
Papaveraceae								
Sanguinaria canadensis	F	0.0	1.4	13.7	8.6	3.0	9.5	0.0
Papaveraceae								
Sanguinaria canadensis	F	0.0	1.4	13.7	8.6	3.0	9.5	0.0
Fumariaceae								
Dicentra cucullaria	F	0.0	0.0	1.8	2.5	0.0	0.0	0.0
Hamamelidaceae								
Hamamelis virginiana	SV	2.1	6.3	10.9	13.2	10.9	2.3	0.0
Ulmaceae								
Celtis occidentalis	T	0.0	0.2	0.3	0.0	0.0	0.2	0.5
Ulmus rubra	T	9.1	23.5	26.5	4.9	10.4	25.0	40.3
Moraceae								
Morus rubra	T	0.0	0.5	0.0	0.2	0.2	0.0	0.2
Urticaceae								
Boehmeria cylindrica	F	0.0	0.2	3.1	0.0	0.0	4.2	0.5
Laportea canadensis	F	0.0	0.0	0.2	0.0	0.0	0.2	0.0
Pilea pumila	F	0.4	5.4	12.8	12.5	5.3	3.7	4.4
Urtica dioica	F	0.6	0.0	0.3	0.0	0.0	1.2	0.0
Juglandaceae								
Carya cordiformis	T	3.2	7.3	10.4	9.5	8.8	5.3	4.9
Carya glabra	T	18.4	16.6	11.0	9.0	22.0	16.7	13.0
Carya ovata	T	1.7	1.5	1.2	1.4	3.7	0.2	0.5
Carya tomentosa	T	4.9	8.1	2.6	9.5	5.1	0.7	5.6
Juglans nigra	T	0.0	0.0	0.3	0.0	0.0	0.2	0.2
Fagaceae								
Fagus grandifolia	T	9.5	10.8	16.9	14.8	12.5	17.6	5.3
Quercus alba	T	35.2	25.7	15.1	24.1	36.6	18.3	20.6
Quercus coccinea	T	10.6	4.9	0.7	6.7	1.4	6.3	6.3
Quercus prinus	T	26.5	11.1	3.3	11.8	13.4	19.4	7.6
Quercus rubra	T	11.2	11.8	9.9	14.8	14.4	8.1	6.5
Quercus velutina	T	25.0	12.8	4.6	17.1	16.2	9.0	12.3
Betulaceae								
Carpinus caroliniana	T	0.4	5.1	11.7	7.9	7.2	3.2	5.6
Corylus americana	SV	2.5	6.6	4.9	9.3	8.1	0.9	0.7
Ostrya virginiana	T	11.9	8.4	2.8	2.5	0.0	0.0	27.5
Phytolaccaceae								
Phytolacca americana	F	0.0	0.2	0.0	0.0	0.0	0.0	0.2
Portulaceae								
Claytonia virginiana	F	0.8	4.7	10.2	19.4	0.0	0.0	2.3
Caryophyllaceae								
Paronychia canadensis[b]	F	0.0	0.2	0.0	0.0	0.2	0.0	0.0
Silene stellata	F	1.3	2.9	0.5	4.4	1.6	0.2	0.0
Silene virginica	F	0.4	0.2	0	0.2	0.5	0.0	0.0
Stellaria pubera	F	0.0	0.3	5.1	7.6	0.0	0.0	0.0
Polygonaceae								
Polygonum persicaria[a]	F	0.0	0.7	0.0	0.0	0.0	0.0	0.9
Polygonum scandens	F	0.0	1.0	0.0	0.0	1.4	0.0	0.0
Polygonum virginianum	F	0.2	5.2	9.0	9.0	4.2	1.2	5.8

Appendix cont.

SPECIES	Life Form	IMI class			Study Area			
		Xeric	Intermediate	Mesic	Watch Rock	Arch Rock	Young's Branch	Bluegrass Ridge
		Percent			Percent			
Clusiaceae								
Hypericum spp.	F	0.0	0.8	0.2	0.5	0.9	0.0	0.0
Tiliaceae								
Tilia americana	T	0.4	0.3	1.0	0.7	0.2	1.4	0.0
Violaceae								
Hybanthus concolor	F	0.0	0.3	0.0	0.5	0.0	0.0	0.0
Viola affinis	F	1.3	0.0	0.0	1.6	0.0	0.0	0.0
Viola blanda	F	0.0	0.0	1.0	0.0	1.4	0.0	0.0
Viola canadensis	F	0.0	0.3	2.3	3.2	0.5	0.0	0.0
Viola pensylvanica	F	0.0	0.2	2.1	2.1	0.0	0.0	1.2
Viola sororia	F	0.0	1.7	3.1	4.4	0.2	0.0	2.1
Viola spp.	F	18.0	32.8	36.7	36.1	33.1	22.7	26.6
Viola striata	F	0.0	0.0	0.2	0.2	0.0	0.0	0.0
Viola triloba	F	17.6	24.5	24.7	16.9	31.7	16.0	25.2
Passifloraceae								
Passiflora lutea	F	0.4	1.4	1.5	0.0	0	1.2	3.2
Brassicaceae								
Cardamine douglassii	F	0.0	1.0	2.5	4.9	0.0	0.0	0.0
Cardamine hirsuta[ab]	F	0.0	0.3	0.2	0.0	0.7	0.0	0.0
Dentaria laciniata	F	3.6	19.4	18.9	19.9	10.6	23.4	3.7
Dentaria heterophylla	F	1.3	5.1	9.2	7.4	1.4	3.5	9.3
Ericaceae								
Chimaphila maculata	F	8.3	5.6	1.2	2.5	2.8	5.6	8.6
Gaultheria procumbens	F	0.2	0.0	0.0	0.0	0.2	0.0	0.0
Gaylussacia baccata	SV	0.2	0.0	0.0	0.0	0.0	0.2	0.0
Oxydendrum arborea	T	5.9	4.1	1.6	6.3	3.7	4.2	0.9
Vaccinium angustifolium	SV	0.9	0.0	0.0	0.0	0.0	1.2	0.0
Vaccinium palidum	SV	47.9	15.2	1.2	21.1	22.0	27.8	10.2
Vaccinium stamineum	SV	12.7	6.4	0.7	6.0	3.9	8.1	7.2
Pyrolaceae								
Pyrola rotundifolia	F	0.0	0.2	1.8	2.5	0.2	0.0	0.0
Monotropaceae								
Monotropa hypopithys	F	0.2	0.0	0.2	0.2	0.2	0.0	0.0
Monotropa uniflora	F	3.4	2.7	1.6	4.2	3.5	2.1	0.5
Primulaceae								
Lysimachia quadriflora	F	3.0	9.8	4.8	9.3	6.7	6.0	1.9
Hydrangeaceae								
Hydrangea arborescens	SV	0.9	4.7	19.2	8.1	10.4	14.6	1.6
Grossulariaceae								
Ribes spp.	SV	0.2	0.0	0.3	0.5	0.0	0.2	0.0
Crassulaceae								
Sedum ternatum	F	1.7	0.3	4.1	3.7	2.5	0.9	1.2
Saxifragaceae								
Heuchera americana	F	0.6	1.5	1.5	0.7	1.4	0.5	2.3
Tiarella cordifolia	F	0.0	1.4	33.9	22.2	23.4	3.0	0.9
Rosaceae								
Agrimonia spp.	F	4.0	6.9	5.3	1.4	5.3	4.9	10.2
Amelanchier arborea	T	23.3	7.4	6.9	9.7	12.0	16.7	10.0
Crataegus spp.	T	13.6	10.5	9.0	15.5	12.0	5.3	10.9
Geum spp.	F	1.1	2.7	4.1	3.0	3.2	0.5	4.2
Porteranthus stipulatus	F	8.0	1.7	0.0	0.7	5.3	2.5	3.5

Appendix cont.

SPECIES	Life Form	IMI class			Study Area			
		Xeric	Intermediate	Mesic	Watch Rock	Arch Rock	Young's Branch	Bluegrass Ridge
		Percent			Percent			
Potentilla canadensis	F	16.1	19.6	9.2	17.4	19.2	8.6	14.4
Prunus serotina	T	11.4	12.2	7.4	10.2	10.4	8.1	12.3
Prunus spp.	SV	0.9	0.5	0.2	0.0	0.0	0.2	1.9
Pyrus coronaria	T	1.9	0.0	0.0	2.3	0.0	0.0	0.0
Rosa carolina	SV	23.3	12.8	5.4	16.4	16.2	7.2	13.9
Rosa multiflora[a]	SV	0.0	1.5	1.3	1.9	1.4	0.0	0.7
Rosa setigera	SV	0.0	0.2	0.0	0.0	0.0	0.0	0.2
Rosa spp.	SV	2.1	0.7	0.3	0.2	0.5	0.7	2.5
Rubus spp.	SV	21.4	26.7	14.3	22.9	28.9	12.3	18.8
Caesalpiniaceae								
Cercis canadensis	T	18.2	22.0	9.0	1.4	4.2	17.4	42.1
Fabaceae								
Amphicarpaea bracteata[b]	F	19.3	21.8	16.4	10.2	28.2	15.7	22.5
Apios americana	F	0.0	0.0	0.2	0.2	0.0	0.0	0.0
Clitoria mariana	F	0.0	0.2	0.0	0.0	0.2	0.0	0.0
Desmodium glutinosum	F	4.9	15.2	13.3	12.3	26.9	3.7	2.8
Desmodium nudiflorum	F	42.6	53.7	36.2	31.9	55.1	58.3	31.3
Desmodium rotundifolium	F	0.0	0.5	0.0	0.0	0.0	0.0	0.7
Lespedeza hirta	F	0.4	0.0	0.0	0.0	0.2	0.2	0.0
Lespedeza spp.	F	4.2	1.2	0.2	0.7	2.1	1.4	2.8
Vicia caroliniana	F	3.0	3.5	0.7	0.0	0.0	1.2	8.3
Onagraceae								
Circaea lutetiana	F	3.6	5.1	17.3	7.2	6.5	12.5	9.5
Cornaceae								
Cornus alternifolia	SV	0.2	0.7	2.0	0.7	0.2	3.0	0.0
Cornus florida	T	44.1	38.7	28.6	23.1	34.7	43.3	46.1
Nyssa sylvatica	T	20.3	15.0	19.7	20.1	22.7	16.4	13.9
Celastraceae								
Celastrus scandens	SV	2.1	2.9	4.8	3.0	2.8	2.1	5.3
Euonymous atropurpureus	SV	0.0	0.8	0.8	0.7	0.2	0.5	0.9
Euphorbiaceae								
Acalypha virginica[b]	F	1.1	3.0	0.3	0.7	2.8	0.0	2.5
Euphorbia corollata	F	0.4	0.0	0.0	0.0	0.2	0.0	0.2
Rhamnaceae								
Ceanothus americanus	SV	0.4	0.0	0.0	0.0	0.5	0.0	0.0
Vitaceae								
Parthenocissus quinquifolius	SV	26.3	48.1	42.4	21.3	36.3	35.6	64.6
Vitis spp.	SV	20.8	25.0	15.6	15.5	18.8	19.2	28.2
Staphyleaceae								
Staphylea trifolia	SV	0.0	0.3	1.0	1.6	0	0.2	0.0
Hippocastanaceae								
Aesculus flava	T	0.2	0.5	0.7	0.7	0.9	0.2	0.0
Aceraceae								
Acer rubrum	T	75.9	68.9	56.4	63.2	76.4	76.9	50.2
Acer saccharum	T	5.1	21.3	30.8	10.0	8.8	22.9	37.0
Anacardiaceae								
Toxicodendron radicans	SV	10.8	16.9	14.6	16.7	17.4	4.6	18.3
Rutaceae								
Ptelea trifoliata	SV	0.0	0.2	0.2	0.0	0	0.2	0.2
Oxalidaceae								
Oxalis grandis	F	0.0	1.0	0.5	0.0	2.1	0.0	0.0

Appendix cont.

SPECIES	Life Form	IMI class			Study Area			
		Xeric	Intermediate	Mesic	Watch Rock	Arch Rock	Young's Branch	Bluegrass Ridge
		Percent			Percent			
Oxalis stricta	F	0.0	0.2	1.6	2.3	0.0	0.0	0.2
Oxalis violacea	F	5.5	2.7	0.2	3.5	3.9	1.4	1.9
Geraniaceae								
Geranium maculatum	F	8.0	31.9	61.3	43.5	42.8	32.9	20.6
Balsaminaceae								
Impatiens spp.[b]	F	0.0	2.5	0.3	0.0	0.0	0.0	3.9
Araliaceae								
Panax quinquefolius	F	0.8	1.9	4.1	0.5	1.6	4.2	3.0
Apiaceae								
Angelica venenosa	F	0.8	0.2	0.0	0.5	0.7	0.0	0.0
Cryptotaenia canadensis	F	0.0	0.2	0.8	0.2	1.2	0.0	0.0
Erigenia bulbosa	F	0.0	0.2	0.0	0.2	0.0	0.0	0.0
Osmorhiza claytonii	F	3.0	4.1	18.8	8.6	4.4	9.0	13.7
Sanicula spp.	F	10.2	15.9	14.3	3.9	7.4	12.0	31.0
Taenida integerrima	F	0.4	0.0	0.0	0.0	0.0	0.0	0.5
Thaspium trifoliatum	F	1.3	0.7	0.2	0.2	0.2	0.9	1.4
Apocynaceae								
Apocynum cannabinum	F	0.4	0.2	0.0	0.0	0.0	0.0	0.7
Asclepiadaceae								
Asclepias quadrifolia	F	1.5	0.5	0.8	0.2	1.6	0.2	1.6
Convolvulaceae								
Convolvulaceae spp.	F	1.1	1.4	0.5	0.9	2.3	0.2	0.5
Polemoniaceae								
Phlox divaricata	F	1.3	5.1	7.6	2.3	0.2	3.9	12.7
Phlox subulata	F	0.6	0.0	0.0	0.7	0.0	0.0	0.0
Polemonium reptans	F	0.0	0.2	2.1	0.7	2.3	0.0	0.2
Hydrophyllaceae								
Hydrophyllum canadense	F	0.0	0.0	0.2	0.2	0.0	0.0	0.0
Hydrophyllum macrophyllum	F	0.0	1.2	8.9	9.5	1.2	3.2	0.2
Boraginaceae								
Cynoglossum virginianum	F	1.1	0.8	0.3	0.2	0.9	0.0	1.9
Hackelia virginiana[c]	F	0.0	0.5	0.0	0.0	0.5	0.0	0.2
Verbenaceae								
Phryma leptostachya	F	0.9	2.2	0.7	0.0	0.2	0.2	4.6
Verbena urticifolia	F	0.2	0.7	0.3	0.0	1.6	0.0	0.0
Lamiaceae								
Blephilia hirsuta	F	0.0	0.2	0.5	0.0	0.0	0.7	0.2
Collinsonia canadensis	F	0.6	0.7	8.1	0.5	1.4	10.4	0.7
Cunila oreganoides	F	12.5	1.2	0.0	3.0	6.0	5.8	2.1
Glechoma hederacea[a]	F	0.2	0.0	0.3	0.0	0.5	0.2	0.0
Monarda fistulosa	F	0.8	1.9	9.7	6.7	2.1	6.5	1.9
Salvia lyrata	F	0.0	0.7	0.0	0.0	0.0	0.0	0.9
Scutellaria spp.	F	4.2	7.1	22.4	13.2	17.4	8.6	7.2
Oleaceae								
Fraxinus americana	T	24.2	42.4	36.7	11.8	15.0	34.7	77.8
Scrophulariaceae								
Aureolaria flava	F	0.0	0.2	0.0	0.2	0.0	0.0	0.0
Aureolaria laevigata	F	6.4	1.9	0.2	0.2	1.2	6.9	2.3
Aureolarlia virginica	F	1.5	0.0	0.0	0.2	1.6	0.0	0.0
Pedicularis canadensis	F	0.2	0.2	0.0	0.0	0.0	0.2	0.2

Appendix cont.

SPECIES	Life Form	IMI class			Study Area			
		Xeric	Intermediate	Mesic	Watch Rock	Arch Rock	Young's Branch	Bluegrass Ridge
		Percent			Percent			
Orobanchaceae								
Conopholis americana	F	2.1	3.5	4.3	0.9	2.1	2.8	7.6
Epifagus virginiana	F	0.0	0.2	1.8	0.0	2.5	0.2	0.0
Acanthaceae								
Ruellia caroliniense	F	0.6	0.3	0.0	0.0	0.0	0.0	1.2
Campanulaceae								
Campanula americana[c]	F	0.0	0.0	0.2	0.2	0.0	0.0	0.0
Lobelia inflata[b]	F	0.0	0.3	0.3	0.0	0.0	0.0	0.9
Lobelia puberula	F	0.2	0.2	0.0	0.2	0.2	0.0	0.0
Rubiaceae								
Galium aparine	F	3.6	11.5	15.8	12.3	0.9	7.6	21.5
Galium circazans	F	20.5	24.7	28.9	14.4	24.5	23.4	37.3
Galium concinnum	F	0.0	5.9	10.7	17.6	5.3	0.2	0.0
Galium lanceolatum	F	1.1	0.3	3.6	0.0	6.9	0.0	0.0
Galium triflorum	F	11.7	30.6	37.3	19.9	21.1	26.2	41.7
Hedyotis caerulea	F	2.5	1.2	0.0	0.5	0.9	3.0	0.2
Hedyotis longifolia	F	2.1	0.2	0.0	0.9	0.7	0.0	1.2
Mitchellla repens	F	0.4	0.0	0.0	0.2	0.2	0.0	0.0
Caprifoliaceae								
Lonicera japonica[a]	SV	0.4	0.5	0.3	0.0	0.0	0.0	1.6
Sambucus canadensis	SV	0.9	0.2	0.5	0.0	0.0	1.9	0.2
Triosteum aurantiacum	F	0.8	0.7	0.2	0.0	0.0	0.7	1.4
Viburnum acerifolium	SV	12.9	27.2	33.7	24.5	30.3	30.8	14.8
Viburnum dentatum	SV	0.0	0.0	0.8	0.2	0.9	0.0	0.0
Viburnum prunifolium	SV	3.2	5.1	5.6	8.3	4.9	3.2	2.3
Asteraceae								
Antennaria plantaginifolia	F	7.0	1.0	0.0	2.5	4.6	2.5	0.2
Aster divaricatus	F	2.7	9.5	22.7	12.7	23.4	8.6	3.5
Aster infirmus	F	2.5	0.0	0.0	0.0	0.0	0.7	2.3
Aster macrophyllus	F	0.0	0.0	0.5	0.0	0.7	0.0	0.0
Aster patens	F	0.8	0.3	0.0	0.0	0.7	0.0	0.7
Aster prenanthoides	F	0.2	0.0	0.0	0.0	0.2	0.0	0.0
Aster sagittifolius	F	0.0	0.0	0.2	0.0	0.2	0.0	0.0
Aster schreberi	F	0.0	0.8	0.3	0.0	1.6	0.0	0.0
Aster shortii	F	0.0	0.2	0.0	0.0	0.2	0.0	0.0
Aster simplex	F	0.2	0.2	0.2	0.0	0.7	0.0	0.0
Aster spp.	F	8.3	6.8	10.9	14.6	8.6	6.7	4.9
Aster undulatus	F	2.8	0.5	0.5	0.0	0.0	1.9	3.0
Cacalia atriplicifolia	G	0.0	0.7	0.7	0.5	0.5	0.0	0.9
Coreopsis major	F	3.2	1.5	0.0	0.0	0.0	3.5	2.5
Erechtites hieracifolia[b]	F	1.5	5.9	9.2	8.1	8.3	3.2	3.2
Erigeron spp.	F	0.2	0.3	0.0	0.2	0.2	0.0	0.2
Eupatorium rugosum	F	4.9	13.3	20.2	15.0	8.8	13.9	15.0
Eupatorium spp.	F	2.5	0.3	1.6	0.7	0.5	0.2	4.4
Helianthus divaricatus	F	10.4	5.2	0.8	3.9	5.6	3.7	7.9
Helianthus microcephalus	F	1.3	0.3	0.2	0.0	0.0	0.0	2.3
Hieracium spp.	F	0.8	0.0	0.0	0.9	0.0	0.0	0.0
Hieracium venosum	F	11.7	1.0	0.0	3.5	5.6	5.8	0.9
Krigia biflora	F	0.4	0.3	0.0	0.0	0.2	0.2	0.5
Senecio aureas	F	0.4	0.0	0.0	0.0	0.0	0.0	0.5
Senecio spp.	F	0.2	0.3	0.0	0.0	0.0	0.0	0.7

Appendix cont.

SPECIES	Life Form	IMI class			Study Area			
		Xeric	Intermediate	Mesic	Watch Rock	Arch Rock	Young's Branch	Bluegrass Ridge
		Percent			Percent			
Solidago caesia	F	9.8	15.5	10.0	12.3	24.3	1.2	9.7
Solidago flexicaulis	F	0.6	1.4	8.9	8.6	6.5	0.0	0.0
Solidago spp.	F	3.2	9.8	4.4	14.8	0.2	4.2	4.4
Solidago ulmifolia	F	2.3	0.5	0.2	0.0	0.0	0.0	3.7
Taraxacum officinale[a]	F	0.4	0.0	0.0	0.5	0.0	0.0	0.0
Verbesina alternifolia	F	0.0	0.7	2.5	3.0	0.2	0.7	0.5
Araceae								
Arisaema triphyllum	F	4.4	11.3	34.4	12.0	16.4	29.9	10.9
Commelinaceae								
Tradescantia virginiana	F	2.8	2.2	1.5	5.8	0.2	0.0	2.5
Juncaceae								
Luzula multiflora	G	1.9	0.7	0.0	0.9	1.6	0.2	0.5
Cyperaceae								
Carex albicans	G	0.4	0.2	0.0	0.7	0.0	0.0	0.0
Carex albursina	G	1.5	1.2	5.6	0.0	3.7	5.6	2.1
Carex amphibola	G	0.0	0.0	0.8	0.0	0.0	0.9	0.2
Carex blanda	G	1.5	6.6	3.3	4.6	7.6	0.0	3.2
Carex communis	G	0.0	0.8	0.0	1.2	0.0	0.0	0.0
Carex complanata	G	1.7	0.7	0.0	0.0	0.0	0.2	2.8
Carex digitalis	G	5.3	10.0	9.4	0.7	4.2	10.9	17.6
Carex flaccosperma	G	0.0	2.4	0.0	3.2	0.0	0.0	0.0
Carex gracilescens	G	4.4	11.8	14.8	15.5	20.8	2.3	3.7
Carex gracillima	G	0.4	0.2	0.0	0.2	0.5	0.0	0.0
Carex jamesii	G	0.0	0.0	0.8	1.2	0.0	0.0	0.0
Carex juniperorum	G	0.6	0.0	0.0	0.0	0.0	0.0	0.7
Carex laxiculmis	G	0.0	1.2	0.7	0.0	2.1	0.2	0.2
Carex laxiflora	G	1.7	6.1	1.3	6.7	2.3	1.9	1.4
Carex nigromarginata	G	2.3	0.3	0.0	2.3	0.2	0.7	0.0
Carex oligocarpa	G	0.6	0.7	0.8	0.0	0.0	0.0	2.8
Carex pennsylvanica	G	8.0	2.7	0.5	3.5	5.6	0.5	4.6
Carex platyplhylla	G	0.0	0.0	0.2	0.2	0.0	0.0	0.0
Carex rosea	G	1.5	5.2	3.8	0.0	7.4	1.6	5.3
Carex spp.	G	4.7	9.6	8.7	16.0	4.6	5.1	5.6
Carex sparganioides	G	0.0	1.7	0.8	0.0	1.2	0.0	2.3
Carex umbellata	G	0.6	0.0	0.0	0.5	0.0	0.2	0.0
Carex wildenovii	G	25.8	12.5	1.8	8.6	12.5	10.9	19.2
Scirpus verecundus	G	0.0	0.3	0.0	0.0	0.5	0.0	0.0
Poaceae								
Agrostis perannans	G	0.2	0.0	0.0	0.2	0.0	0.0	0.0
Brachyelytrum erectum	G	7.4	19.3	22.2	20.8	23.6	7.4	14.8
Bromus pubescens	G	3.0	8.3	6.3	2.5	6.7	3.0	11.6
Danthonia spicata	G	10.8	1.4	0.0	4.9	3.9	3.7	2.5
Diarrhena americana	G	1.3	2.2	4.6	2.3	2.8	2.1	3.9
Elymus hystrix	G	2.5	1.7	0.3	0.2	0.7	0.2	4.6
Festuca obstusa	G	0.4	1.5	0.5	0.0	0.0	0.7	2.5
Muhlenbergia teniflora	G	1.3	3.2	0.5	0.0	6.0	0.2	0.5
Panicum boscii	G	19.9	16.7	3.0	11.3	14.8	8.3	16.9
Panicum commutatum	G	1.3	0.3	0.2	0.2	0.0	0.9	1.2
Panicum dichotomum	G	11.6	4.2	0.8	7.9	5.8	6.5	0.9
Panicum latifolium	G	4.5	3.9	2.0	3.7	10.0	0.0	0.0
Panicum linearifolium	G	0.4	0.0	0.0	0.5	0.0	0.0	0.0

Appendix cont.

SPECIES	Life Form	IMI class			Study Area			
		Xeric	Intermediate	Mesic	Watch Rock	Arch Rock	Young's Branch	Bluegrass Ridge
		Percent			Percent			
Panicum spp.	G	5.5	5.6	1.3	12.0	2.5	1.6	0.0
Poa alsodes	G	0.2	0.0	0.0	0.0	0.2	0.0	0.0
Poa cuspidata	G	13.6	15.9	16.1	18.5	25.9	3.7	13.0
Poa nemoralis[a]	G	0.0	0.0	0.8	0.0	1.2	0.0	0.0
Sphenopholis nitida	G	0.4	0.5	0.2	0.5	0.7	0.0	0.2
Liliaceae								
Allium canadense	F	0.0	0.0	0.2	0.2	0.0	0.0	0.0
Chamaelirium luteum	F	0.0	0.7	0.2	0.9	0.2	0.0	0.0
Erythronium spp.	F	0.0	0.0	3.5	4.6	0.0	0.2	0.0
Lilium canadense	F	0.0	0.7	0.3	1.4	0.0	0.0	0.0
Medeola virginiana	F	0.0	4.6	7.1	3.7	5.1	7.4	0.0
Polygonatum biflorum	F	22.9	15.7	6.9	11.1	5.6	14.8	27.8
Smilacinia racemosa	F	21.2	37.5	35.4	26.6	22.2	32.4	45.8
Trillium grandiflorum	F	1.1	6.4	43.4	25.0	20.8	21.5	3.9
Uvularia perfoliata	F	15.0	44.8	53.1	29.6	30.8	46.5	47.5
Smilacaceae								
Smilax ecirrhata	F	1.1	0.5	1.0	0.0	2.5	0.2	0.7
Smilax glauca	SV	37.9	35.8	16.3	29.4	24.3	28.7	35.9
Smilax hispida	SV	2.8	4.4	8.9	3.7	4.9	8.6	4.9
Smilax rotundifolia	SV	58.5	38.7	27.0	29.4	39.4	59.5	34.3
Dioscoreaceae								
Dioscorea quaternata	F	5.1	9.8	21.2	2.1	0.9	35.6	10.9
Dioscorea villosa	F	0.6	1.2	3.1	3.7	3.0	0.0	0.0
Iridaceae								
Iris cristata	F	0.0	0.5	1.5	0.0	0.0	2.8	0.0
Sisyrinchium angustifolium	F	0.0	0.2	0.0	0.0	0.0	0.0	0.2
Orchidaceae								
Corallorhiza odontorhiza	F	0.2	0.0	0.0	0.0	0.2	0.0	0.0
Cypredium acaule	F	0.9	0.0	0.0	0.0	0.0	1.2	0.0
Cyprepedium calceolus	F	0.0	0.2	0.5	0.5	0.2	0.2	0.0
Goodyera pubescens	F	1.9	2.0	2.6	4.2	2.8	1.9	0.0
Liparis lilifolia	F	0.4	0.7	0.2	0.0	0.0	0.0	1.6
Malaxis unifolia	F	0.2	0.0	0.0	0.0	0.2	0.0	0.0
Orchis spectabilis	F	0.8	1.0	2.6	2.1	0.9	2.1	0.9

[a]Non-native.
[b]Annual.
[c]Biennial.

Chapter 8

Composition and Abundance of Tree Regeneration

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Abstract

The composition and abundance of tree seedlings and saplings in the four study areas in southern Ohio were related to soil moisture via a GIS-derived integrated moisture index and to soil texture and fertility. For seedlings, the total abundance of small stems (less than 30 cm tall) was significantly greater on xeric plots (81,987/ha) than on intermediate (54,531/ha) and mesic (42,222/ha) plots. There were 28 species in the seedling layer, the most abundant of which were red maple, sassafras, white ash, and flowering dogwood. Oak seedlings were most abundant on xeric plots (7,195/ha) and least abundant on mesic plots (2,121/ha). Thirty-six species were recorded in the sapling layer; the most abundant were dogwood, red maple, sugar maple, blackgum, and beech. More than 90 percent of the stems in the sapling layer were species classified as shade tolerant or very tolerant. Detrended correspondence analysis indicated that sugar maple, beech, and witch-hazel were associated with fertile, moist sites, red maple and blackgum with less fertile, xeric sites, and dogwood, redbud, and white ash with intermediate sites. Historical data suggest that the current abundance of shade-tolerant species in the sapling layer is a new condition for these forests. The results presented here provide baseline data to test whether the reintroduction of fire can facilitate a shift in the trajectory of succession toward an understory with a higher relative abundance of oak and hickory.

Introduction

Many factors affect the composition of forests. At a regional scale, the distributions of tree species are related to broad patterns of climate, landform, and soil (Iverson et al. 1999). At a smaller scale, disturbance regimes and topographic variation interact to influence species composition.

Tree species vary considerably in life history traits that influence regeneration success under particular environmental conditions (Sutherland et al. 2000). Shade tolerance is one of the most important traits determining establishment, survival, and growth (Loach 1970; Spurr and Barnes 1980). The frequency and magnitude of disturbances (natural or human caused) that influence light availability to the forest floor largely determine which tree species survive and grow into the upper canopy (Lorimer 1980; Peterson and Pickett 1995; Loftis 1990). If disturbances are small in spatial extent and infrequent, shade-tolerant species often become abundant even when the overstory is dominated by less tolerant species (Lorimer 1984; Abrams et al. 1995).

Topographic variation also influences species composition. In the northern hemisphere, solar radiation and temperature are greatest on southwest-facing slopes (SW) and least on northeast-facing slopes (NE), resulting in an environmental gradient of decreasing temperature and evaporative demand and increasing soil moisture from SW to NE (Wolfe et al. 1949; Hutchins et al. 1976; Xu et al. 1997; Stephenson 1998). The topographically generated soil-moisture gradient also affects rates of decomposition and nutrient cycling, with nitrogen-availability greater on mesic, north-facing slopes (Garten et al. 1994; Morris and Boerner 1998). In turn, species composition and productivity are strongly correlated to these aspect-generated gradients of evaporative demand (Lipscomb and Nilson 1990; Stephenson 1998) and to soil moisture and fertility (Muller 1982; Pastor et al. 1984; Fralish 1994; Iverson et al. 1997).

Oak-hickory is the most abundant forest type in the United States (Powell et al. 1993) dominating much of the eastern U.S. landscape for nearly 10,000 years (Webb 1981; Delcourt and Delcourt 1987). In the unglaciated Allegheny plateau of southern Ohio, mixed-oak forest, a

component of the oak-hickory group, was the most abundant forest type prior to Euro-American settlement ca. 1800 (Gordon 1969). Following extensive logging in the 1800s, much of the landscape regenerated to oak dominance (Griffith et al. 1993). However, throughout southern Ohio, forest statistics indicate that the relative abundance of oaks and hickories is declining, while maples (*Acer rubrum*, *Acer saccharum*), black cherry (*Prunus serotina*), and yellow-poplar (*Liriodendron tulipifera*) are increasing (Griffith et al. 1993). Maples now dominate the understory in oak stands of various ages (Goebel and Hix 1996; Norland and Hix 1996; McCarthy et al. 2001). The trends observed in Ohio are similar to those reported for many other oak forests in the eastern United States (Lorimer 1984; Abrams 1992; Loftis and McGee 1993; Schuler and Gillespie 2000). Dendroecology studies indicate that maples have established since 1900 in second-growth (Tift and Fajvan 1999; Schuler and Fajvan 1999) and old-growth oak stands (Abrams et al. 1995; Mikan et al. 1994).

Thick bark allows oak trees to survive surface fires of low to moderate intensity. Also, seedlings and saplings that are topkilled can resprout repeatedly (Lorimer 1985; Crow 1988; Abrams 1992; Hengst and Dawson 1994). However, under closed-canopy forests that are relatively undisturbed, oak seedlings are less abundant (Carvell and Tryon 1961), seedling growth is slow (Buckley et al.1998), and mortality is high (Crow 1992; Lorimer et al. 1994). Oaks have also failed to regenerate following several methods of timber harvesting (Schuler and Miller 1995; Jenkins and Parker 1998). Other species that have thinner bark and allocate more resources to aboveground biomass, such as red maple, sugar maple, and yellow-poplar, are negatively affected by fire (Hengst and Dawson 1994; Kruger and Reich 1997; Brose et al. 1999). These traits of oaks and other species have led to the hypothesis that fire suppression in the 20th century has been the primary cause of the widespread dominance by shade-tolerant and/or fire-sensitive species in the understory layer of oak forests (Lorimer 1985; Abrams 1992). Other factors cited as reducing the abundance of oak regeneration include acorn predation by deer, rodents, and insects, and browsing of seedlings by deer (Buckley et al. 1998; Galford et al. 1991).

In 1994, a multidisciplinary research project was initiated in southern Ohio to study the effectiveness of prescribed fire as a tool to restore structure, composition, and function to second-growth mixed-oak forests. Here we quantify patterns of seedling and sapling composition and abundance prior to prescribed fire treatments. Specifically, we examine variation in the regeneration layer across a topographic moisture gradient and among four study areas that are fairly similar in land-use history (see Chapter 2) but differ somewhat in geomorphology (Chapter 4), soil characteristics (Chapter 5), and overstory composition (Chapter 9).

Methods

Study Areas and Experimental Design

The study areas and experimental design are described in detail in Chapter 1. Here a brief overview is provided. The four 75-90 ha study areas are located in Vinton County (Arch Rock and Watch Rock) and Lawrence County (Young's Branch and Bluegrass Ridge). The study areas are within in the Southern Unglaciated Allegheny Plateau, which is characterized by high hills, sharp ridges, and narrow valleys. Sandstones and shales are principle bedrocks. Forests are oak-dominated and the current overstory originated in the late-1800s, after the cessation of clearcutting for the charcoal iron industry.

In each study area, three prescribed fire treatments were established, a control unit (CONT), an infrequent burn unit (INFR), and a frequent burn unit (FREQ). To account for variation in soil moisture and vegetation, a GIS-derived integrated moisture index (IMI) was applied across the dissected landscapes of the study areas (Chapter 3). From the calculated IMI scores, each 30 x 30 m pixel was assigned to one of three soil moisture classes: xeric, intermediate, or mesic. Thus to examine the effects of prescribed fire and account for environmental heterogeneity, a split-plot experimental design was established. The four study areas are replicate blocks, fire treatment units are whole plots, and IMI classes are subplots. The 50 x 25 m vegetation plots (N= 108 total) were established as pseudoreplicates in each IMI class within each fire treatment unit (Chapter 1).

Vegetation Sampling

One regeneration plot was located in a 25- by 25-m portion of each vegetation plot and consisted of a sapling subplot (312.5 m^2) and two circular (0.8-m-radius) seedling subplots (2 m^2 each). The IMI for each regeneration plot was calculated from the four corners of the 25- by 25-m plot, resulting in 40 plots classified as xeric, 32 as intermediate, and 36 as mesic (Chapter 3).

In the seedling subplots, stems of all living woody species were recorded in three size classes, small (1 to 30 cm tall), medium (30.1 to 100 cm), and large (100.1 to 137 cm), from June to August 1995. Data from the two 2-m^2 seedling subplots were averaged to obtain seedling abundance per plot for summary statistics. Only seedlings of trees and tall shrub species (frequently more than 137 cm tall) are reported here. Seedlings were marked permanently with wire of three different gauges to indicate size class. From June to August 1995 in the sapling plots, all living stems 1.37 m tall to 9.9 cm in diameter at breast height (d.b.h.) were tallied by species in three classes: small (1.37 m tall to 2.9 cm d.b.h.), medium (3.0 to 5.9 cm d.b.h.), and large (6.0 to 9.9 cm d.b.h.).

Table 1.--Mean number of seedlings per hectare (± 1 standard error) among IMI classes and study areas by size class (seedling density averaged from two 2-m² subplots for each plot).

		IMI class			Study area		
	Total	Xeric	Intermediate	Mesic	WR	AR	YB	BR
Size class	(N = 108)	(N = 40)	(N = 32)	(N = 36)	(N = 27)	(N = 27)	(N = 27)	(N = 27)
Small	60397	81987	54531	42222	48750	43889	57129	91389
(0 to 30 cm)	(4952)	(10572)	(6776)	(5327)	(7665)	(5249)	(6586)	(14766)
Medium	5841	6859	5703	4861	5865	3425	5185	8889
(30.1 to 100 cm)	(651)	(1146)	(1152)	(1077)	(1028)	(945)	(998)	(1836)
Large	1893	1538	1641	2500	1923	1667	2037	1944
(100.1 to 137 cm)	(265)	(299)	(429)	(606)	(506)	(462)	(534)	(631)

Table 2.--Analysis of variance (ANOVA) testing for significant differences in the abundance of seedlings and saplings among IMI classes and treatment units (the ANOVA was a mixed model with study area as random effect and IMI and treatment units as fixed effects).

Item	Source	F	P
	Seedlings		
Small	Treatment	1.23	0.357
(1 to 30 cm)	IMI	5.09	0.018[a]
	Treatment X IMI	0.93	0.47
Medium	Treatment	1.52	0.293
(30.1 to 100 cm)	IMI	2.56	0.105
	Treatment X IMI	0.74	0.579
Large	Treatment	4.26	0.071
(100.1 to 137 cm)	IMI	1.58	0.234
	Treatment X IMI	1.09	0.389
	Saplings		
Small	Treatment	2.08	0.206
(137 cm tall	IMI	0.98	0.396
to 2.9 cm d.b.h.)	Treatment X IMI	2.95	0.049[b]
Medium	Treatment	0.90	0.456
(3.0 to 5.9 cm d.b.h.)	IMI	0.57	0.576
	Treatment X IMI	0.58	0.681
Large	Treatment	0.38	0.70
(6.0 to 9.9 cm d.b.h.)	IMI	2.38	0.121
	Treatment X IMI	0.73	0.649

[a]Xeric plots had significantly more small seedlings than intermediate and mesic plots (LS means < P = 0.05).
[b]There were significant differences among several treatment X IMI categories.

Data Analysis

A mixed-model analysis of variance (PROC MIXED) was used to test for significant differences in seedling and sapling density among the three IMI categories and pretreatment differences among the three fire-treatment units (SAS 1996). The study areas were treated as random effects and IMI and treatment units as fixed effects.

We used detrended correspondence analysis (DCA) to examine community variation in the sapling layer (PC-Ord Vers. 3.0; McCune and Mefford 1997). DCA is a multivariate technique that uses a weighted-averaging algorithm to simultaneously calculate plot and species scores that are plotted in ordination space. In the ordination diagram, species are located near the plots in which they are common and plots are located near the species of which they are composed. Input data included the relative density of each species per plot. Rare species were downweighted.

Results

Seedling Abundance and Composition

Small, medium, and large seedlings averaged 60,397, 5,841, and 1,893 stems per ha, respectively (Table 1). Small seedlings averaged 81,987 stems/ha on xeric plots; this amount was significantly greater than on intermediate (54,531) and mesic (42,222) plots (Table 2). There were no significant IMI effects on the densities of medium and large seedlings, nor were there pretreatment differences in total seedling abundance among the three fire-treatment units (Table 2). The abundance of small seedlings was greatest at BR (91,389 stems/ha) and least at AR and WR, which averaged 43,889 and 48,750 stems/ha respectively.

Twenty-eight species were sampled in the small-seedling class (Table 3). Sample sizes were small for medium and large classes and are not summarized here. The most abundant species were red maple (13,750 stems/ha) sassafras (*Sassafras albidum*; 10,556/ha), white ash *(Fraxinus americana;* 7,546/ha), and flowering dogwood (*Cornus florida*; 5,440/ha) (Table 3). Oak seedlings (all size classes) averaged 4,352/ha; there were significantly more on xeric plots (7,195/ha) than on mesic plots (2,121/ha) ($F = 3.73$, $P = 0.044$; Fig. 1b). There were no significant differences in oak seedling density among treatment units ($F = 0.78$, $P = 0.501$; Fig. 1a). Among the oaks, white (*Quercus alba*) was the most abundant (2,269/ha), followed by chestnut (*Q. prinus*), black (*Q. velutina*), red oak (*Q. rubra*), and scarlet oak (*Q. coccinea*) (Table 3). Other species that averaged more than 1,000 seedlings/ha included yellow-poplar, slippery elm (*Ulmus rubra*), serviceberry (*Amelanchier arborea*), and sourwood (*Oxydendrum arborea*).

The most abundant species on xeric plots were red maple, sassafras, serviceberry, white oak, sourwood, and chestnut oak (Table 3). White ash, flowering dogwood, and yellow-poplar were the most abundant on intermediate plots and slippery elm and sugar maple were the most abundant on mesic plots. Species abundance also varied among the four study areas. Many of the common species were most abundant at BR. These included sassafras, white ash, slippery elm, serviceberry, sourwood, and sugar maple. The three most common oaks, white, chestnut, and black, were most abundant at AR study area (Table 3).

Sapling Abundance and Composition

Small, medium, and large saplings averaged 1,631, 426, and 208 stems/ha, respectively (Table 4). For all size classes, sapling abundance was highest on intermediate IMI plots, but the differences were not statistically significant (Table 2). There were no pretreatment differences in total sapling abundance among the fire-treatment units (Table 2). The abundance of small saplings was greatest at BR (1,837/ha), followed by YB (1,719/ha), AR (1,540/ha), and WR (1,431/ha).

Thirty-six species were recorded, 22 of which can attain overstory stature (Table 5). Nearly 60 percent of saplings (mean density per ha) were flowering dogwood (516.8 stems/ha), red maple (393.6), and sugar maple (378.3). Also abundant were blackgum (228.5 stems/ha) and American beech (*Fagus grandifolia*, 208.9/ha). White ash, witch-hazel (*Hamamelis virginiana*), redbud (*Cercis canadensis*), and slippery elm had densities exceeding 45 stems/ha.

Of these common species, red maple and blackgum were the most abundant on xeric plots, flowering dogwood, witch-hazel, redbud, and slippery elm on intermediate plots; sugar maple, American beech and white ash were the most abundant on mesic plots (Table 5). Species abundance also varied among the study areas. Flowering dogwood, sugar maple, and slippery elm were more common at the Lawrence County sites (YB and BR) and witch-hazel and blackgum were more abundant at the Vinton County sites (AR and WR) (Table 5).

Common species in the overstory (see Chapter 9) that averaged fewer than 20 saplings/ha were mostly oaks, including black (13.6), chestnut (13.4), white (8.0), red (6.8), and scarlet (0.3). Overall, oak sapling density was significantly higher on xeric plots (96.5/ha) than on intermediate (10.3 per/ha) and mesic (14.0/ha) plots ($F = 4.28$, $P = 0.030$; Fig. 1d). The density of oak saplings was similar among treatment units, averaging 49.8, 36.8, and 34.2 on control, infrequent, and frequent units, respectively ($F = 0.120$, $P = 0.888$; Fig. 1c). The density of hickories (*Carya* spp.) and yellow-poplar also was higher in the overstory than in the sapling layer.

Shade-tolerant or very tolerant species accounted for more than 90 percent of saplings per plot (Fig. 2). Common tolerant species included red maple, redbud, blackgum, sourwood, and slippery elm. Very tolerant common species included sugar maple, American hornbeam (*Carpinus caroliniana*), flowering dogwood, and American beech. Species that are intermediate in shade tolerance accounted for only 8.7 percent of the average relative stem density. These included four of the five oaks, all of the hickories, and white ash (Fig. 2). Intolerant species averaged less than 1 percent of relative density. The relative density of intermediate species was greater on xeric (14.0 percent) than intermediate (5.0) and mesic (6.2) plots. Conversely, very tolerant species were more abundant on mesic than xeric plots, averaging 68.4 and 38.5 percent relative density, respectively. The relative densities of very tolerant species were greatest at BR (72.9 percent) and YB (60.1 percent) largely because of the greater abundance of flowering dogwood and sugar maple (Fig. 2).

DCA indicated that soil fertility and moisture were the primary environmental factors correlated to sapling composition (Fig. 3, Table 6). Axis 1 represented the primary gradient describing variation in sapling composition (eigenvalue = 0.606) and axis 1 plot scores were positively correlated with soil pH (0.581), NO_3^- (0.570), nitrification rate (0.567), nitrogen mineralization rate (0.561), and IMI (0.512) (Table 6). Most of the plots with the lowest axis 1 scores were xeric IMI plots and most of the plots with the highest axis 1 scores were mesic IMI plots (Fig. 3a). However, there was significant overlap in sapling composition among the IMI classes (Fig. 3a).

Table 3.--Mean number of small (1 to 30 cm) seedlings per hectare among IMI classes and study areas, by species (species with fewer than 100 seedlings per hectare are not included).

		IMI class			Study area			
Species	Total (N=108)	Xeric (N=40)	Inter-mediate (N=32)	Mesic (N=36)	Watch Rock (N=27)	Arch Rock (N=27)	Young's Branch (N=27)	Bluegrass Ridge (N=27)
Acer rubrum	13750	20250	12969	7222	14907	14259	19444	6389
Sassafras albidum	10556	22938	4141	2500	6574	7593	7870	20185
Fraxinus americana	7546	5313	9141	8611	741	926	3056	25463
Cornus florida	5440	2938	8906	5139	5093	3982	8241	4444
Liriodendron tulipifera	3727	3750	5078	2500	6111	740	5000	3056
Ulmus rubra	3264	1688	3750	4583	648	1482	2500	8426
Amelanchier arborea	2569	4625	1875	903	1389	2222	1574	5093
Quercus alba	2269	3438	1719	1458	1389	3982	1389	2315
Oxydendron arborea	1759	4500	78	208	370	648	0	6019
Quercus prinus	1111	2313	313	486	926	2037	1296	185
Acer saccharum	926	313	1172	1389	463	556	556	2130
Quercus velutina	879	1375	1173	69	648	1481	741	648
Nyssa sylvatica	764	750	547	972	741	926	1111	277
Cercis canadensis	694	563	1406	208	0	278	463	2037
Carya glabra	648	750	938	278	556	556	741	741
Quercus rubra	602	875	703	208	648	370	556	833
Crataegus spp.	509	250	781	556	278	463	1296	0
Prunus serotina	370	625	78	347	463	278	185	556
Carya cordiformis	324	125	391	486	463	463	93	278
Carpinus caroliniana	255	375	78	278	278	93	0	648
Carya tomentosa	232	375	234	69	185	185	185	370
Ostrya virginiana	162	188	0	278	93	0	0	556
Viburnum prunifolium	139	0	0	417	556	0	0	0
Quercus coccinea	116	188	156	0	0	0	370	93

Table 4.--Mean number of saplings per hectare (± 1 standard error) among IMI classes and study areas, by size class.

		IMI class			Study area			
Species	Total (N=108)	Xeric (N=40)	Inter-mediate (N=32)	Mesic (N=36)	Watch Rock (N=27)	Arch Rock (N=27)	Young's Branch (N=27)	Bluegrass Ridge (N=27)
Small	1631	1706	1763	1432	1431	1540	1719	1837
(1.37 m tall to 2.9 cm d.b.h.)	(90.3)	(135.8)	(217.0)	(114.6)	(124.5)	(164.7)	(141.5)	(260.4)
Medium	426	438	468	375	353	375	427	549
(3.0 to 5.9 cm d.b.h.)	(18.8)	(27.9)	(36.3)	(33.6)	(34.1)	(36.2)	(34.1)	(36.2)
Large	208	207	241	180	166	187	239	239
(6.0 to 9.9 cm d.b.h.)	(9.6)	(16.7)	(16.0)	(15.9)	(17.5)	(17.4)	(17.9)	(20.9)

Table 5. — Mean densities of species in the sapling size classes among IMI classes and study areas. Species that have the potential to obtain overstory stature are in bold print.

Species	Sz	Total	IMI Class			Study Area			
			Xer	Int	Mes	WR	AR	YB	BR
		N=108	N=40	N=32	N=36	N=27	N=27	N=27	N=27
		Stems per hectare							
Cornus florida	S	384.9	423.2	525.0	217.8	80.6	174.2	539.3	745.5
COFL	M	98.4	103.2	129.0	65.8	43.9	51.0	126.8	171.9
Flowering dogwood	L	33.5	37.6	41.0	22.2	17.8	22.5	49.8	43.9
Acer rubrum	S	267.6	378.4	301.0	114.7	180.1	399.4	214.5	276.1
ACSA	M	74.7	83.2	87.0	54.2	52.1	90.1	66.4	90.1
Red maple	L	51.3	40.8	73.0	43.6	43.9	67.6	69.9	23.7
Acer saccharum	S	253.0	104.0	248.0	423.1	149.3	168.3	298.7	395.9
ACRU	M	80.0	42.4	99.0	104.9	36.7	28.4	68.7	186.1
Sugar maple	L	45.3	30.4	55.0	53.3	27.3	9.5	28.4	116.1
Nyssa sylvatica	S	131.3	214.4	86.0	79.1	202.7	216.9	90.1	15.4
NYSY	M	64.6	108.8	44.0	33.8	80.6	83.1	79.4	14.2
Blackgum	L	32.6	46.4	28.0	21.3	32.0	41.5	46.2	10.7
Fagus grandifolia	S	158.2	110.4	156.0	213.3	175.4	145.8	243	68.7
FAGR	M	39.4	28.8	34.0	56.0	59.3	62.8	24.9	10.7
American beech	L	11.3	7.2	9.0	17.8	14.2	21.3	4.7	4.7
Fraxinus americana	S	60.7	59.2	58.0	64.9	68.7	34.4	81.8	58.1
FRAM	M	5.6	6.4	6.0	4.4	3.6	7.1	3.6	8.3
White ash	L	2.7	1.6	3.0	3.6	0.0	3.6	4.7	2.4
Hamamelis virginiana	S	62.2	46.4	79.0	64.9	162.4	86.5	0.0	0.0
HAVI	M	4.2	0.0	11.0	2.7	13.0	2.4	1.2	0.0
Witch hazel	L	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cercis canadensis	S	38.8	48.0	67.0	3.6	0.0	83.0	23.7	48.6
CECA	M	10.4	7.2	21.0	4.4	0.0	17.8	11.9	11.9
Redbud	L	3.3	1.6	9.0	0.0	0.0	5.9	3.6	3.6
Ulmus rubra	S	35.3	5.6	80.0	28.4	4.7	4.7	73.5	58.1
ULRU	M	8.9	2.4	19.0	7.1	1.2	7.1	11.9	15.4
Slippery elm	L	2.7	0.8	4.0	3.6	2.4	2.4	2.4	3.6
Carpinus caroliniana	S	24.9	24.8	21.0	28.4	23.7	7.1	9.5	59.3
CACA	M	7.7	5.6	7.0	10.7	5.9	0.0	10.7	14.2
American hornbeam	L	0.6	0.8	0.0	0.9	0.0	0.0	1.2	1.2
Carya tomentosa	S	22.8	42.4	15.0	8.0	30.8	28.4	2.4	29.6
CART	M	4.2	8.0	1.0	2.7	9.5	3.6	2.4	1.2
Mockernut hickory	L	2.4	4.0	2.0	0.9	3.6	0.0	1.2	4.7
Asimina triloba	S	27.6	0.0	52.0	36.4	43.9	0.0	66.4	0.0
ASTR	M	0.6	0.0	2.0	0.0	0.0	0.0	2.4	0.0
Paw paw	L	0.3	0.0	1.0	0.0	0.0	0.0	1.2	0.0
Oxydendrum arboreum	S	22.5	45.6	8.0	9.8	27.3	37.9	19.0	5.9
OXAR	M	1.2	3.2	0.0	0.0	2.4	0.0	2.4	0.0
Sourwood	L	3.0	8.0	0.0	0.0	2.4	7.1	1.2	1.2
Viburnum prunifolium	S	22.2	19.2	1.0	44.4	85.3	0.0	3.6	0.0
VIPR	M	2.1	0.8	0.0	5.3	8.3	0.0	0.0	0.0
Black haw	L	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 5. cont.

Species	Sz	Total N=108	IMI Class Xer N=40	Int N=32	Mes N=36	Study Area WR N=27	AR N=27	YB N=27	BR N=27
				Stems per hectare					
Liriodendron tulipifera	S	21.3	21.6	14	27.6	52.1	17.8	9.5	5.9
LITU	M	1.5	0.8	1	2.7	4.7	0	0	1.2
Yellow poplar	L	0.9	1.6	1	0	1.2	0	1.2	1.2
Amelanchier arborea	S	15.4	23.2	12	9.8	15.4	17.8	20.1	8.3
AMAR	M	3.6	4	2	4.4	3.6	2.4	8.3	0
Serviceberry	L	1.8	2.4	0	2.7	0	0	7.1	0
Sassafras albidum	S	11	16.8	13	2.7	9.5	7.1	7.1	20.1
SAAL	M	3.6	8.8	1	0	0	0	0	14.2
Sassafras	L	2.4	4.8	2	0	0	0	2.4	7.1
Carlya glabra	S	10.7	22.4	3	4.4	10.7	22.5	7.1	2.4
CARG	M	3.3	7.2	1	0.9	8.3	1.2	3.6	0
Pignut hickory	L	2.4	4	2	0.9	4.7	0	4.7	0
Quercus velutina	S	12.4	32	0	1.8	22.5	23.7	1.2	2.4
QUVE	M	0.9	1.6	0	0.9	3.6	0	0	0
Black oak	L	0.3	0.8	0	0	1.2	0	0	0
Quercus prinus	S	6.2	16	0.8	0.9	7.1	16.6	0	1.2
QUPR	M	3.3	8	0	0.9	4.7	5.9	0	2.4
Chestnut oak	L	3.9	9.6	0	0.9	7.1	2.4	3.6	2.4
Tilia americana	S	7.7	0.8	2	20.4	14.2	11.9	3.6	1.2
TIAM	M	2.4	0	2	5.3	3.6	2.4	2.4	1.2
American basswood	L	1.8	0	2	3.6	1.2	1.2	4.7	0
Quercus alba	S	2.4	4.8	1	0.9	4.7	2.4	0	2.4
QUAL	M	1.2	2.4	0	0.9	2.4	2.4	0	0
White oak	L	4.4	4.8	7	1.8	3.6	1.2	0	13
Ostrya virginiana	S	5.6	6.4	3	7.1	5.9	1.2	0	15.4
OSVI	M	1.5	0.8	1	2.7	1.2	2.4	0	2.4
Eastern hophornbeam	L	0	0	0	0	0	0	0	0
Aesculus flava	S	4.7	1.6	6	7.1	5.9	8.3	0	4.7
AEFL	M	1.2	0	0	3.6	0	3.6	0	1.2
Yellow buckeye	L	0.9	0	0	2.7	3.6	0	0	0
Quercus rubra	S	5.3	11.2	1	2.7	7.1	13	0	1.2
QURU	M	0.9	1.6	0	0.9	2.4	0	0	1.2
Northern red oak	L	0.6	0	2	0	0	1.2	1.2	0

Species occurring at <5 stems/ha include *Corylus americana* (4.1), *Crataegus spp.* (3.6), *Juglans nigra* (1.2), *Castanea dentata* (1.2), *Prunus serotina* (0.6), *Carya cordiformis* (0.6), *Morus rubra* (0.3), *Quercus coccinea* (0.3), *Pyrus coronaria* (0.3), *Rhus spp.* (0.3), and *Acer negundo* (0.3).

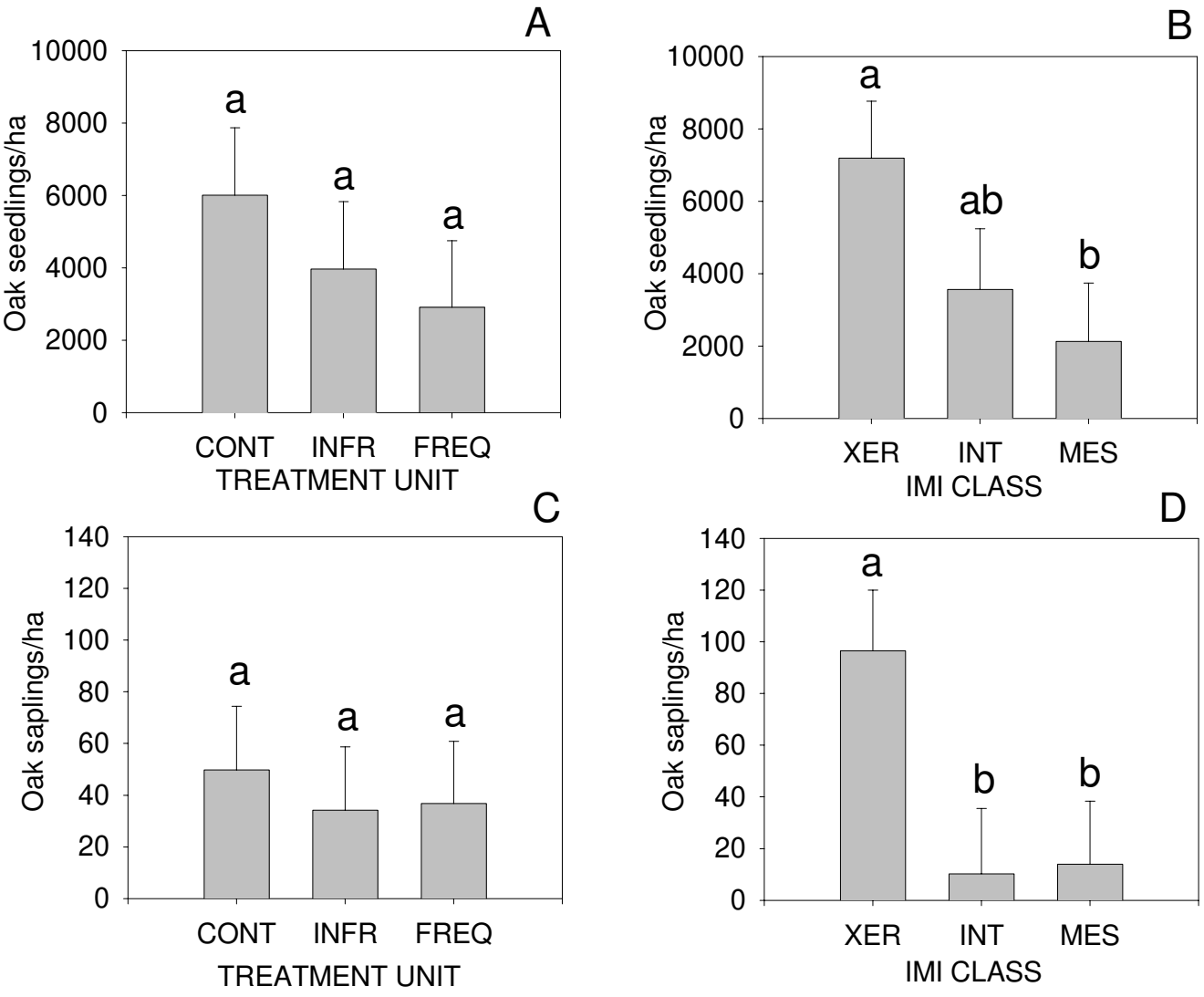

Figure 1. -- A. Oak seedling densities among the treatment units (CONT = control; INFR = infrequent; FREQ = frequent), prior to treatment; B. Oak seedling densities among the three IMI (moisture) classes (XER = xeric; INT = intermediate; MES = mesic); C. Oak sapling densities among the treatment units; D. Oak sapling densities among the IMI classes. Seedlings were stems < 1.37 m height and saplings were 1.37 m in height to 9.9 cm diameter at breast height. In each graph, letters that are different indicate statistically significant ($p < 0.05$) differences among classes (ANOVA).

Common species with high axis 1 scores that were associated with the most fertile and moist sites included sugar maple, American beech, and witch-hazel (Fig. 3c). Species near the center of axis 1 occurred over a wide range of soil conditions and included white ash, redbud, and dogwood. Red maple and blackgum had lower axis 1 scores and thus were associated with plots lower in fertility and moisture (Fig. 3c). Uncommon species associated with the least fertile sites included the oaks and hickories while paw paw (*Asimina triloba*) and American basswood (*Tilia americana*) were associated with fertile, moist sites (Fig. 3c).

A secondary gradient along axis 2 (eigenvalue = 0.367) indicated variation in species composition among study areas. Watch Rock and AR plots generally had lower axis 2 scores, BR plots had higher scores, and YB plots were intermediate (Fig. 3b). Common species with high axis 2 scores (associated with the BR plots) included redbud and dogwood. Witch-hazel and American beech had low axis 1 scores (associated with the WR and AR plots). Axis 2 plot scores were positively correlated with soil PO_4^- and percent sand, but only at r = 0.441 and 0.404, respectively (Table 6).

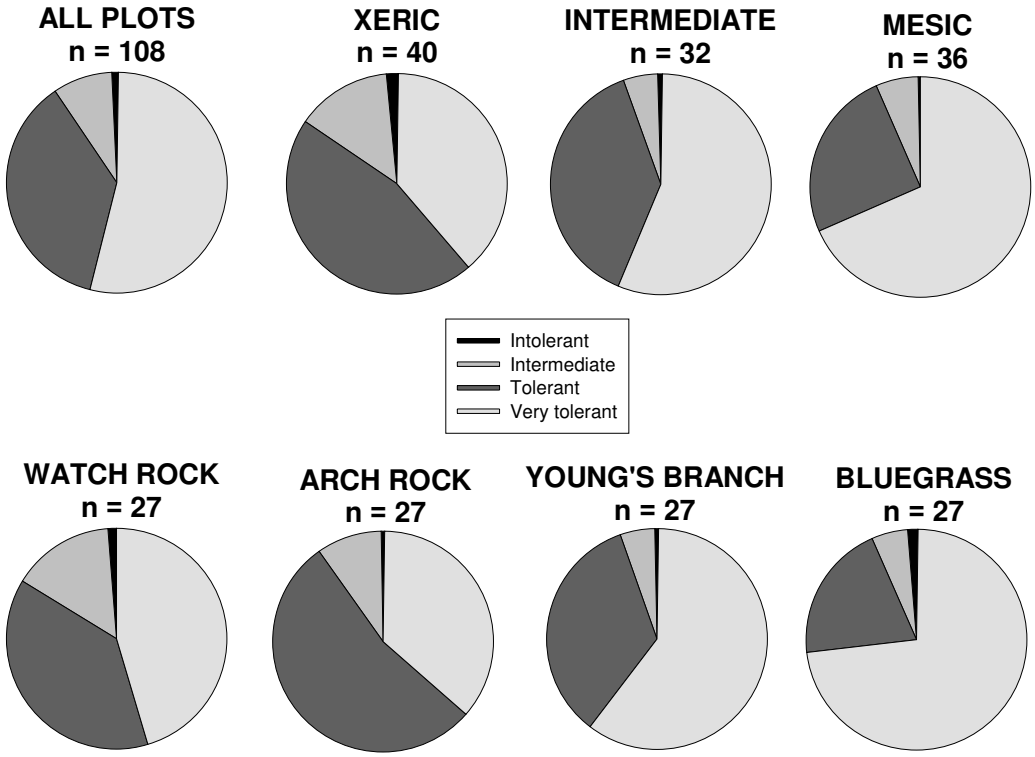

Figure 2.-- Relative density of sapling groups based on shade tolerance classifications. All sapling size classes were combined and species that cannot attain overstory stature (e.g. dogwood) are included. Shade tolerance classifications were from Burns and Honkala (1990), Iverson et al. (1999), and Sutherland et al. (2000).

Discussion

The total abundance of small seedlings averaged 60,397/ha, which is within the range reported in other eastern oak forests (Abrams and Nowacki 1992; Goebel and Hix 1997; Arthur et al. 1998). Competition from dense herbaceous vegetation may have limited seedling densities on mesic plots where seedlings were least abundant, particularly where fern cover was high (George and Bazzaz 1999). Red maple was the most abundant species in the small-seedling class. Although not abundant in the overstory, it was a common midstory tree (10 to 20 cm d.b.h.) in all study areas (Chapter 9), produces abundant seed at an early age, and can germinate under a variety of conditions, including shaded understories with hardwood litter cover (Burns and Honkala 1990). Sassafras was the most abundant seedling species on xeric sites but was rare in the tree size classes, indicating a persistent seedling bank. Other species that were uncommon in the overstory but that occurred at relatively high seedling densities included white ash, red elm, sugar maple, and black cherry. Seeds of these species germinate well when the seedbed is moist, shaded, and covered with litter (Burns and Honkala 1990), a common condition in these relatively undisturbed forests.

The abundance of oak seedlings was fairly similar to that of a variety of oak forests in the Eastern United States (Carvell and Tryon 1961; Schuler and Miller 1995; Host et al. 1987; Rebertus and Burns 1997). However, oak seedling densities of nearly 140,000/ha have been reported (Carvell and Tryon 1961) and a study by Schuler and Fajvan (1999) suggests that oak seedling densities have decreased on mesic sites since the early 1900s. The observed decrease in the abundance of oak seedlings from xeric to mesic sites has been well documented (e.g., Carvell and Tryon 1961; Host et al. 1987; Jenkins and Parker 1998). Although the density of competing species in the sapling layer was least on mesic plots, competition from the dense herbaceous vegetation may have reduced oak seedling stocks (Carvell and Tryon 1961). Our data indicate that oak seedling abundance also corresponded with the relative basal area of oak, which averaged 87.1, 71.1, and 50.8 percent on xeric, intermediate, and mesic plots, respectively (Chapter 9).

Although the seedling subplots were distributed widely over 108 plots in a large geographic area, the sampling intensity per plot was small (two 2-m^2 subplots), resulting in high variability and a small sample of seedlings more than 30 cm tall. In addition to the abundance data presented here, the frequency of seedlings in sixteen 2-m^2 quadrats per plot is reported in Chapter 7.

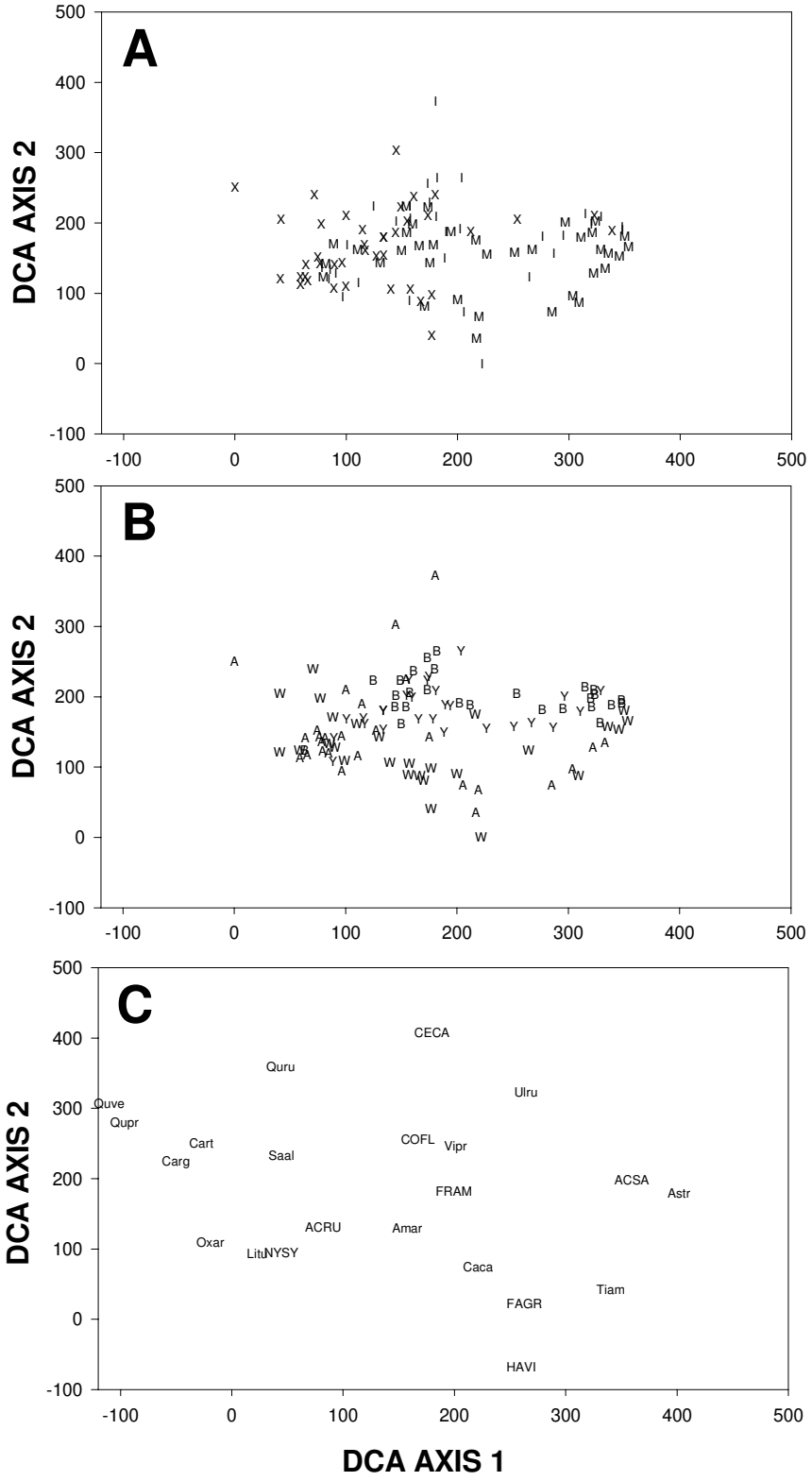

Figure 3.--Detrended correspondence analysis of the sapling subplots. A. Ordination of the 108 plots classified by IMI: X = xeric, I = intermediate, and M = mesic. B. Ordination of the 108 plots classified by study area: A= Arch Rock, W = Watch Rock, Y = Young's Branch, and B = Bluegrass Ridge. C. Ordination of species in the sapling layer. Species that occurred at a mean density of greater than 50 stems per hectare are abbreviated in all capital letters and species that averaged 10 to 50 stems per hectare are abbreviated with small letters following the first letter. Species that averaged less than 10 stems per hectare are not shown in the graph. Species names for the abbreviations are listed in Table 5.

Table 6. — Pearson correlations between the 13 environmental variables and the DCA plot scores for the saplings.

Variable	Axis 1[a]	Axis 2[a]	Axis 3[a]
pH	0.581	0.189	0.078
NO_3^-	0.570	-0.024	0.238
Nitrification rate	0.567	0.186	0.139
N mineralization rate	0.561	-0.089	0.300
IMI	0.512	-0.230	0.244
NH_4^+	0.438	-0.091	0.241
PO_4^-	0.367	0.441	-0.089
Percent sand	0.172	0.404	-0.062
Stand age	-0.010	-0.050	0.081
Tree basal area	-0.050	0.071	-0.156
Percent silt	-0.163	-0.385	0.093
Global light index	-0.245	0.073	0.159

[a]eigenvalues = 0.606 for axis 1, 0.367 for axis 2, and 0.222 for axis 3

Total sapling density was similar to that in several mixed-oak forests of similar age and land-use history in the region (Abrams and Nowacki 1992; Goebel and Hix 1997; McCarthy et al. 2001). DCA indicated that variation in sapling composition was related to pH, N availability, and IMI along axis 1. Because light levels varied little and were universally low, light availability was weakly correlated to sapling composition. Our results suggest that low light availability may be the primary factor influencing seedling survival and growth rates, resulting in a relatively homogeneous sapling layer dominated by several shade-tolerant species. However, there was variation in the abundance of shade tolerant species across the moisture gradient. Red maple and blackgum (tolerant) were associated with xeric plots while sugar maple and beech (very tolerant) were most abundant in mesic areas. Flowering dogwood (very tolerant) was common everywhere and most abundant on intermediate plots. These results correspond to the successional trends documented in many eastern oak forests for red maple (Lorimer 1984; Host et al. 1987; Abrams and Nowacki 1992; Goebel and Hix 1996), sugar maple (Eickmeier 1988; Lorimer et al. 1994; Jenkins and Parker 1998; Schuler and Gillespie 2000), and blackgum (Rhoades 1992; Arthur et al. 1998; Harrod et al. 1998). For southern Ohio, our results indicate a successional trend that is presumably new to these sites. Witness-tree data indicate that shade-tolerant species were relatively minor components of the forest prior to Euro-American settlement (Chapter 2).

Oaks were the dominant canopy species, and although oak seedlings were fairly abundant, saplings were rare. In Wisconsin oak forests, Lorimer et al. (1994) reported that densities and growth of oak seedlings were improved significantly by the removal of a dense sapling layer. The use of prescribed fire to regenerate oaks has shown mixed results (e.g., Wendel and Smith 1986; Barnes and Van Lear 1998). However, shelterwood harvests followed by high-intensity fires have improved oak regeneration on productive upland sites in Virginia (Brose et al. 1999). A primary goal of our study is to document large-scale, long-term effects of frequent and infrequent fire on oak regeneration (Chapter 1).

One of the central goals of ecosystem management is sustainability (Christensen et al. 1996). Under current disturbance regimes, the species composition of mixed-oak forests in southern Ohio probably cannot be sustained. Forest management that includes the use of prescribed fire may be needed to perpetuate oak ecosystems in this region. The results presented here provide baseline data with which to test whether the reintroduction of fire may shift the trajectory of succession toward an understory with a higher relative abundance of oak and hickory.

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Chapter 9

Structure, Composition, and Condition of Overstory Trees

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Abstract

The structure, composition, and condition of overstory trees in the four study areas prior to prescribed fire treatments are summarized. Stand initiation dates were similar among the study areas (ca. 1885), and coincided with the decline of the charcoal iron industry in southern Ohio. Tree basal area averaged 26.8m^2/ha and was not significantly different among Integrated Moisture Index classes. Tree density averaged 378 trees/ha and was highest on xeric plots (407/ha). Diameter growth averaged 3.6 mm/year and was greatest in areas with higher concentrations of soil nitrogen or base cations. Branch dieback was 20 percent or less for 96 percent of the 4,894 overstory trees, and foliage transparency was 20 percent or less for about 90 percent of the trees, indicating good crown condition. Twenty-nine species were recorded, the most abundant of which were white oak (79 trees/ha), red maple (52.9/ha), chestnut oak (49.2/ha), hickories (37/ha), and sugar maple (31.6/ha). Despite the abundance of red maple and sugar maple, most of these trees were in the smaller diameter classes (10 to 25 cm d.b.h.), suggesting more recent recruitment in the stands. Although oaks continue to dominate the overstory of these stands, the abundance of shade-tolerant species in the smaller size classes indicates consistent successional trends across the landscape, particularly on intermediate and mesic sites.

Introduction

More than half of the land area in southeastern Ohio is forested, with oak-hickory the most abundant forest type (Griffith et al. 1993). Although located within Braun's (1950) mixed mesophytic forest region, the "Low Hills Belt" in southeastern Ohio is dominated by oak-hickory forests. The assessment of Griffith et al. agrees with the record of witness trees from which Gordon (1969) classified most of southern and eastern Ohio as mixed-oak forest (ca. 1800). Indeed, studies of fossil pollen indicate that oaks have dominated the forests of this region for at least 5,000 years (Ogden 1966; Delcourt and Delcourt 1987; Delcourt et al. 1998). Prior to significant Euro-American settlement in the Ohio Valley, travelers and early settlers frequently described forests that were park-like, with large, widely spaced overstory trees and relatively little undergrowth of woody vegetation (see Chapter 2). The use of fire by Native Americans also was described, so it is likely that many primary forests in the region experienced anthropogenic fires in addition to grazing and browsing by quadrupeds such as deer, elk, and bison (Williams 1989; Whitney 1994; Chapter 2).

Currently, most mature second-growth forests in the Central Hardwoods Region are dominated by a mixed-oak overstory that developed between the mid-1800s and the early 1930s as subsistence farming and charcoal production for iron ore smelting declined (Hicks 2000). The overstory at each of our study areas originated following clearcutting to produce charcoal used in iron smelting in the mid-19th century. The iron industry declined in the late 1800s (Chapter 2).

A dendroecological study of fire scars in a second-growth stand (Vinton County, OH) indicated that dormant-season fires were frequent from 1870 to 1930 (Sutherland 1997); similar results were observed in stands throughout southern Ohio (Sutherland, unpublished). The seedlings, saplings, and trees that survived the fires became today's overstory, which is dominated by oak species on most upland landscapes. The most abundant oak species in the region are white oak (*Quercus alba*), chestnut oak (*Q. prinus*), scarlet oak (*Q. coccinea*), northern red oak (*Q. rubra*), and black oak (*Q. velutina*) (Iverson et al. 1999). These forests also can include 25 or more canopy and subcanopy species other than oaks (Beatley 1959). Other common tree species in the overstory include hickory (*Carya spp.*), yellow-poplar

(*Liriodendron tulipifera*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), ash (*Fraxinus spp.*), and black cherry (*Prunus serotina*) (Griffith et al. 1993).

Recently, species associated with mesic sites and species that are considered sensitive to fire have become more abundant in oak-dominated forests across the region (Abrams 1992). Natural mortality caused by drought, insects, disease, or windthrow is less than 5 percent annually (Stringer et al. 1989). Recruitment of stems into canopy gaps rarely is by oak species (Runkle 1998; McCarthy et al. 2001). In sharp contrast to descriptions of presettlement forests, the secondary forests have a dense midstory layer dominated by maples and other shade-tolerant species (Chapter 9).

Because the observed successional trends in the region have coincided with a decrease in the frequency and spatial extent of fire since the mid-20th century (Yaussy and Sutherland 1993; Sutherland 1997), prescribed burning is being evaluated as a tool to restore the structure, composition, and function to mixed-oak forests. In this chapter we quantify the baseline structure, composition, condition, and productivity of the overstory across a moisture gradient and among the four study areas prior to prescribed fire treatments.

Methods

Study Areas and Experimental Design

The study areas and experimental design are described in detail in Chapter 1. Here a brief overview is provided. The four 75-90 ha study areas are located in Vinton County (Arch Rock and Watch Rock) and Lawrence County (Young's Branch and Bluegrass Ridge). The study areas are within in the Southern Unglaciated Allegheny Plateau, which is characterized by high hills, sharp ridges, and narrow valleys. Sandstones and shales are principle bedrocks. Forests are oak-dominated and the current overstory originated in the late-1800s, after the cessation of clearcutting for the charcoal iron industry.

In each study area, three prescribed fire treatments were established, a control unit (CONT), an infrequent burn unit (INFR), and a frequent burn unit (FREQ). To account for variation in soil moisture and vegetation, a GIS-derived integrated moisture index (IMI) was applied across the dissected landscapes of the study areas (Chapter 3). From the calculated IMI scores, each 30 x 30 m pixel was assigned to one of three soil moisture classes: xeric, intermediate, or mesic. Thus to examine the effects of prescribed fire and account for environmental heterogeneity, a split-plot experimental design was established. The four study areas are replicate blocks, fire treatment units are whole plots, and IMI classes are subplots. The 50 x 25 m vegetation plots (N= 108 total) were established as pseudoreplicates in each IMI class within each fire treatment unit (Chapter 1).

Field Methods

In the first year of data collection (January-April, 1995), species, status (alive or dead) and d.b.h. (diameter at breast height, 1.4 m) were recorded for all standing trees at least 10.0 cm d.b.h. Each tree was marked permanently. For each tree, we also recorded whether it was on the regeneration or the understory subplot. These measurements indicate conditions present at the end of the 1994 growing season and are termed "1994" data. The "1995" measurements were taken from January to April 1996, when measurements were collected to evaluate stand age, diameter growth, stand dynamics (ingrowth, tree mortal status, crown position), tree health (crown condition: foliage transparency and branch dieback), and potential economic value (grade). D.b.h. was remeasured and mortality determined for all trees. Ingrowth trees were identified, painted, and tagged.

Crown class (Helms 1998) and potential tree grade (Yaussy 1993) were recorded for live trees larger than 24 cm in diameter after the 1997 growing season. Stem quality consisted of four grades that each tree would likely attain when it reached a d.b.h. of 40 cm. Grade 1 had the fewest knots, seams, and other defects while grade 4 had the most defects.

Crown condition was evaluated by estimating foliage transparency and branch dieback on all living trees in summer of 1995 following Millers et al. (1991). Foliage transparency is an estimate of the amount of light passing through the crown, and describes crown density for given species as well as accounting for reduced foliage density resulting from herbivory, disease, or other injurious agents. Hence, the foliage density or the amount of light passing through the crown (transparency) for a healthy tree of one species may be considerably lower than that for a healthy tree of another species, so the measure is most useful for within-species comparisons. Branch dieback is a measure of recent branch mortality that begins at the terminal portion of a limb and progresses downward. Presumably, branch dieback reflects some stress (e.g., drought, herbivory) on the tree and is not species-specific, though some species may be more susceptible to a given stress than others.

Increment cores were collected in October and November 1996, to determine the age of the stands and develop tree-ring chronologies from the sites. Two of the largest trees outside the plots but within 10 m of opposite plot corners were selected. Favored in order was the white oak group, the red oak group, and other trees. For each tree, two cores were taken with an increment borer at a height of 1 m; species and d.b.h. also were recorded. The cores were

Table 1.—Summary statistics for overstory variables on the 108 plots in four study areas.

Item	Minimum	25%	Mean	Median	75%	Maximum
D.b.h. (cm)	9.9	14.3	26.5	22.9	36.2	102.0
1-year d.b.h. growth (mm)	0.0	2.0	3.6	3.0	5.0	22.0
Trees/ha (no.)	224.0	320.0	378.2	368.0	424.0	664.0
Basal area (m^2/ha)	16.6	24.3	26.8	27.0	29.2	37.5
Basal area in oak (%)	4.4	57.9	69.3	75.7	88.7	99.1
Foliage transparency (%)	5.0	10.0	11.7	10.0	10.0	100.0
Branch dieback (%)	2.0	10.0	8.1	10.0	10.0	90.0
Crown class	1.0	2.0	3.0	3.0	4.0	4.0
Age (years)	64.0	94.0	110.2	109.0	129.0	154.0
Mortality (1 year) (%)	0.0	1.9	3.9	3.2	5.6	12.8
Tree grade	1.0	2.0	2.4	2.0	3.0	4.0

glued in grooved, wooden mounts and sanded with progressively finer grits of sandpaper for accurate dating and measurement of rings. If the pith was not included in either core (per tree), both cores were used to estimate the pith age in a 5-year class. To determine the age of each plot, we chose the oldest of the two trees sampled unless we judged that the older tree was not representative of the overall stand age. This occurred twice when one tree per plot was more than 200 years old. These were residual trees that were not harvested during the charcoal iron period.

Data Analysis

A mixed-model analysis of variance (ANOVA) was used to test for significant differences in overstory characteristics among the three IMI categories and pretreatment differences among the three treatment units (SAS 1999). The study areas were treated as blocked random effects and IMI and treatment units as fixed effects. Values less than 0.05 were considered significant and P-values greater than 0.05 and less than 0.10 were considered marginally significant.

Results

Age, Structure and Productivity

Of the 216 trees cored (mean d.b.h. = 40.8 cm), 121 were white oak, 39 chestnut oak, 16 black oak, 14 northern red oak, 8 yellow-poplar, 6 scarlet oak, 5 hickory, 4 sugar maple, and 1 each of post oak (*Quercus stellata*), ash, and red maple. Overall, the mean stand age was 110.2 (Table 1). The YB study area had the oldest stands (average plot age = 120.9 years) with nearly half of the plots being at least 140 years old (Table 2). Stand age did not differ significantly among IMI classes (F = 0.38, p = 0.688) but was marginally different among fire-treatment units (F = 3.70, p = 0.088; Table 3).

Tree density and basal area averaged 378.2 trees/ha and 26.8 m^2/ha, respectively (Table 1). Tree density was greatest at YB (416 trees/ha) and on xeric plots (407.1 trees/ha), though the difference among IMI classes was marginally significant (F = 3.24, p = 0.058; Tables 2-3). Tree basal area was similar among the study areas, with WR averaging slightly less (25.3 m^2/ha) than the other sites, which ranged from 27.1 to 27.8 m^2/ha (Table 2). Basal area was not significantly different among IMI classes (F = 0.92, p = 0.418; Table 3) or among fire-treatment units (F = 1.48, p = 0.277). The relative abundance of suppressed trees averaged 39.2 percent versus 27.7 percent for codominant, 17.6 percent for intermediate, 8.6 percent for standing dead, and 6.9 percent for dominant trees (Table 4). The average score for crown class did not differ among IMI classes (F = 1.88, p = 0.180) or fire-treatment units (F = 0.04, p = 0.960) (Table 3).

Diameter growth averaged 3.6 mm from the 1994 to 1995 growing seasons (Table 3). Diameter growth was marginally different among the IMI classes (F = 3.39, p = 0.051). Trees in the intermediate plots had a higher growth rate (4.0 $\pm$ .07 mm/yr [mean $\pm$ 1 SE]) than those in the mesic (3.5 $\pm$ .07 mm/yr) and xeric (3.3 $\pm$ .06 mm/yr) plots (Tables 2, 4). Diameter growth was also higher at WR (4.2 $\pm$ .08 mm/yr) and BR (4.1 $\pm$ .09 mm/yr) than at AR (3.1 $\pm$ .06 mm/yr) and YB (3.1 $\pm$ .07 mm/yr). One-year rates of mortality (1994-1995 growing seasons) averaged 3.9 percent and were not significantly different among IMI classes (F = 1.00, p = 0.383) or fire-treatment units (F = 0.33, p = 0.719) (Tables 3-4). However, mortality was highest at AR, averaging 5.3 percent compared to 3.3 to 3.8 percent in the other study areas (Table 2).

Table 2.—Means for overstory variables among the four study areas and three IMI classes.

Item	WR	AR	BG	YB	Xeric	Interm.	Mesic
D.b.h. (cm)	25.94	27.39	27.54	25.44	26.20	27.04	26.35
1-year d.b.h. growth (mm)	4.18	3.09	4.09	3.13	3.29	4.04	3.45
Trees/ha (no.)	368.00	374.81	354.07	416.00	407.06	366.95	362.89
Basal area (m^2/ha)	25.30	27.18	27.11	27.82	27.17	27.36	26.01
Basal area in oak (%)	68.89	72.47	68.98	67.05	87.05	71.07	50.81
Foliage transparency (%)	13.22	13.36	10.34	9.85	12.21	11.24	11.51
Branch dieback (%)	13.58	14.04	11.40	10.81	13.09	12.29	11.86
Crown class	3.05	2.92	2.96	3.05	2.95	2.98	3.03
Age (years)	111.78	107.70	100.30	120.85	113.12	110.45	107.06
Mortality (1 year) (%)	3.75	5.28	3.42	3.32	3.30	4.06	4.42
Tree grade	2.42	2.40	2.37	2.40	2.50	2.31	2.37

Species Composition

We recorded 29 tree species (Table 5), the most abundant of which were white oak (79 trees/ha), red maple (52.9/ha), chestnut oak (49.2/ha), hickory (37/ha), sugar maple (31.6/ha), black oak (24/ha), and yellow-poplar (20.7/ha). White oak, sourwood (*Oxydendron arborea*), and black oak had the most standing dead trees/ha, averaging 7.4, 5, and 3.7, respectively.

The relative abundance of white oak was high in all moisture classes and in the larger size classes but it exhibited lower relative abundance in the 10- to 30-cm size classes, particularly in the mesic areas (Fig. 1). Despite the abundance of red maple in all study areas and IMI classes, nearly all of the trees were less than 25 cm in d.b.h. Sugar maple showed a similar size distribution but was rare on xeric plots. Chestnut oak was most abundant on xeric plots but uncommon in the 10-to 20-cm class. Hickories (*Carya glabra*, *C. tomentosa, C. cordiformis, C. ovata*) were more abundant on intermediate and mesic sites and in the 20- to 40-cm d.b.h. class. Black oak was abundant in all moisture classes but uncommon in size classes less than 30 cm d.b.h.

Although other species were common in the smaller and intermediate size classes, oaks accounted for a high percentage of the stand basal area (overall mean = 69.3 percent) due to their high relative abundance in the larger size classes (Table 1, Fig. 1). The proportion of basal area in oak was significantly different among IMI classes ($F = 30.2$, $p < 0.001$), averaging 87.1, 71.1, and 50.8 percent on xeric, intermediate, and mesic plots, respectively (Tables 2-3). The percentage of basal area in oak did not differ significantly among fire-treatment units ($F = 1.48$, $p = 0.277$).

Differences in size class distributions among species also are evident in the relative percentages of trees in the four crown classes. For the white oak group (white oak and chestnut oak) and the red oak group (black oak, northern red oak, scarlet oak) nearly 50 percent and nearly 75 percent of the trees, respectively, were codominant or dominant (Fig. 2). Yellow-poplar was the only other common species with half or more of its trees in these two classes. Among the common species that can attain dominant or codominant status, half or more of the stems of red maple, sugar maple, ash, blackgum, and miscellaneous overstory species (e.g., beech, [*Fagus grandifolia*]) were in the suppressed category (Fig. 2).

Crown Condition

Foliage transparency was 20 percent or less in virtually every tree (mean = 11.7%). Branch dieback also was 20 percent or less in 96 percent of trees (mean = 8.1%). These low percentages were found across all size and crown classes (Tables 2, 5). Foliar transparency was higher at WR and AR (13.2 and 13.4 percent, respectively) than at YB and BR (9.9 and 10.3 percent) and was significantly different among IMI classes ($F = 4.99$, $p = 0.019$) but not fire-treatment units ($F = 0.72$, $p = 0.525$) (Tables 2-3). Branch dieback showed the same pattern, i.e., higher at WR and AR (13.6 and 14.0 percent) than at YB and BR (10.8 and 11.4 percent), and marginally different among IMI classes ($F = 3.50$, $p = 0.051$), but not fire-treatment units ($F = 0.51$, $p = 0.625$). For both transparency and dieback, average values were highest on xeric plots (Table 2). Most species had a majority of trees in the excellent class for transparency and dieback, though less than half of the trees in the red oak group were in the excellent category for both variables (Figs. 3-4). Tree grades were significantly higher (indicating more defects) on xeric plots ($F = 7.29$, $p = 0.005$) but did not differ significantly among fire-treatment units ($F = 1.82$, $p = 0.214$) (Table 3).

Table 3. -Analysis of variance for significant differences in overstory variables among the treatment units, IMI classes, and interactions.

Item	Source	F-value	p-level
D.b.h. (cm)	Treatment	2.52	0.104
	IMI	0.37	0.698
	Trt*IMI	1.58	0.216
1-year d.b.h. growth (mm)	Treatment	1.72	0.201
	IMI	3.39	0.051
	Trt*IMI	1.12	0.373
Trees/ha (no.)	Treatment	3.08	0.066
	IMI	3.24	0.058
	Trt*IMI	0.40	0.805
Basal area (m2/ha)	Treatment	0.20	0.825
	IMI	0.92	0.418
	Trt*IMI	2.72	0.065
Basal area in oak (%)	Treatment	1.48	0.277
	IMI	30.19	0.000
	Trt*IMI	1.91	0.158
Foliage transparency (%)	Treatment	0.72	0.525
	IMI	4.99	0.019
	Trt*IMI	1.49	0.248
Branch dieback (%)	Treatment	0.51	0.625
	IMI	3.50	0.051
	Trt*IMI	0.28	0.888
Crown class	Treatment	0.04	0.960
	IMI	1.88	0.180
	Trt*IMI	0.30	0.872
Age (years)	Treatment	3.70	0.088
	IMI	0.38	0.688
	Trt*IMI	0.05	0.996
Mortality (1 year) (%)	Treatment	0.33	0.719
	IMI	1.00	0.383
	Trt*IMI	1.44	0.253
Tree grade	Treatment	1.82	0.214
	IMI	7.29	0.005
	Trt*IMI	0.33	0.855

Discussion

The majority of the even-aged stands on the four study areas originated in the mid- to late-1800s, which coincides with the decline in the charcoal iron industry across the region. Because the forests have developed on terrain with similar geomorphology and land use, it is not surprising that forest structure and composition are similar across the study sites.

Tree basal area averaged 27 m^2/ha, which was nearly identical to second-growth stands of similar age in southeastern Ohio (Goebel and Hix 1996) and somewhat less than the 30 to 32 m^2/ha values reported for several old-growth oak-hickory forests in the Midwest (Whitney 1994). Tree density, which averaged 378 trees/ha, was greater than that reported for old growth oak-hickory forests (320 to 350 trees/ha). However, the density of presettlement forests may have been lower than current old-growth forests based on early descriptions of more open-structured forests.

By definition, mesic plots had higher predicted soil moisture, and also had more available inorganic N (NH_4 and NO_3), and higher pH than intermediate plots (see Chapter 5), but diameter growth was significantly greater on intermediate plots. However, the latter had more soil Ca, Mg, and P than mesic plots. This might explain the greater diameter-growth rates (e.g., Long et al. 1997).

Differences in diameter growth among the study areas may also be related to soil fertility. Diameter growth was about 35 percent higher at WR and BR than at AR and YB despite similar average IMI values for the plots among the study areas (Chapter 3). The soils data suggest that greater soil N availability drove higher diameter growth at WR. For a variety of oak forests, Reich et al. (1997) showed a strong and positive linear relationship between nitrogen availability (nitrogen mineralization rate) and productivity. At BR, higher diameter growth may be related to significantly greater soil Ca, Mg, and Ca:Al ratios, the result of the interbedded limestone strata at that site (Chapter 4). However, the higher diameter-growth rates on intermediate plots and at WR and BR did not result in greater basal area at those sites.

Stand structure did not differ significantly across the moisture gradient, though, as expected, patterns of species abundance differed among IMI classes. For the most abundant species, white oak and red maple were ubiquitous across the landscape, while chestnut oak and black oak were the most abundant on xeric and xeric/intermediate sites, respectively. Hickory, sugar maple, and yellow-poplar were most abundant on intermediate and mesic sites. Compositional change across the IMI classes was evident in the tree regeneration layer (Chapter 8), and particularly in the understory vegetation layer (Chapter 7). Aspect-driven gradients in species composition are typical for forests in the region (Hutchins et al. 1976; Muller 1982; Goebel and Hix 1996).

Our results indicate that the current composition of the overstory is similar to that of the presettlement forests in the area, which were dominated by several oak (especially white oak) and hickory species (Chapter 2). However, strong successional trends also are apparent as shade-tolerant species including red maple, sugar maple, and

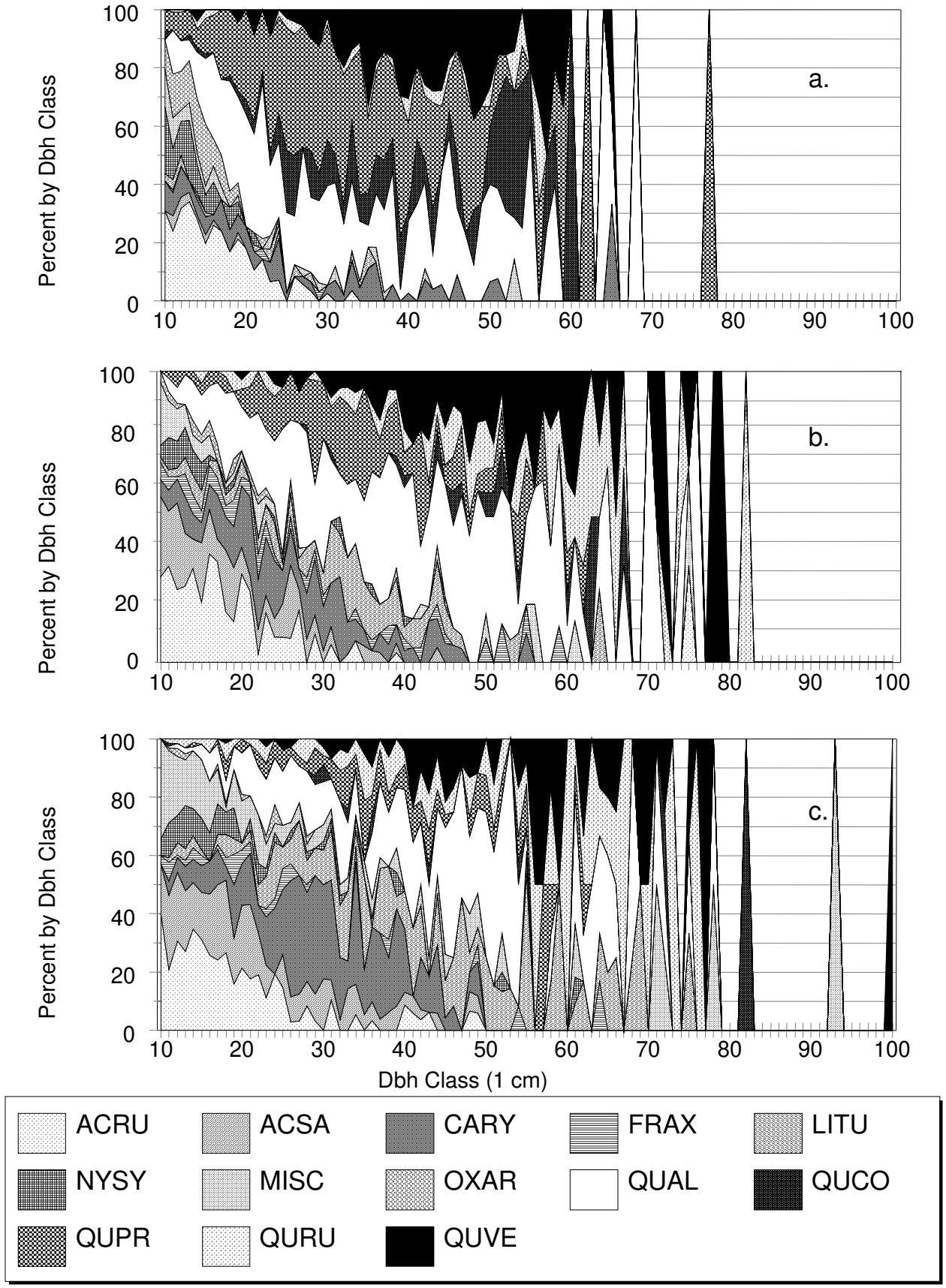

Figure 1.—Percentage of trees by diameter class (1 cm) and IMI class, (a=xeric, b=intermediate, c=mesic). Species included in the miscellaneous group are listed in Table 5.

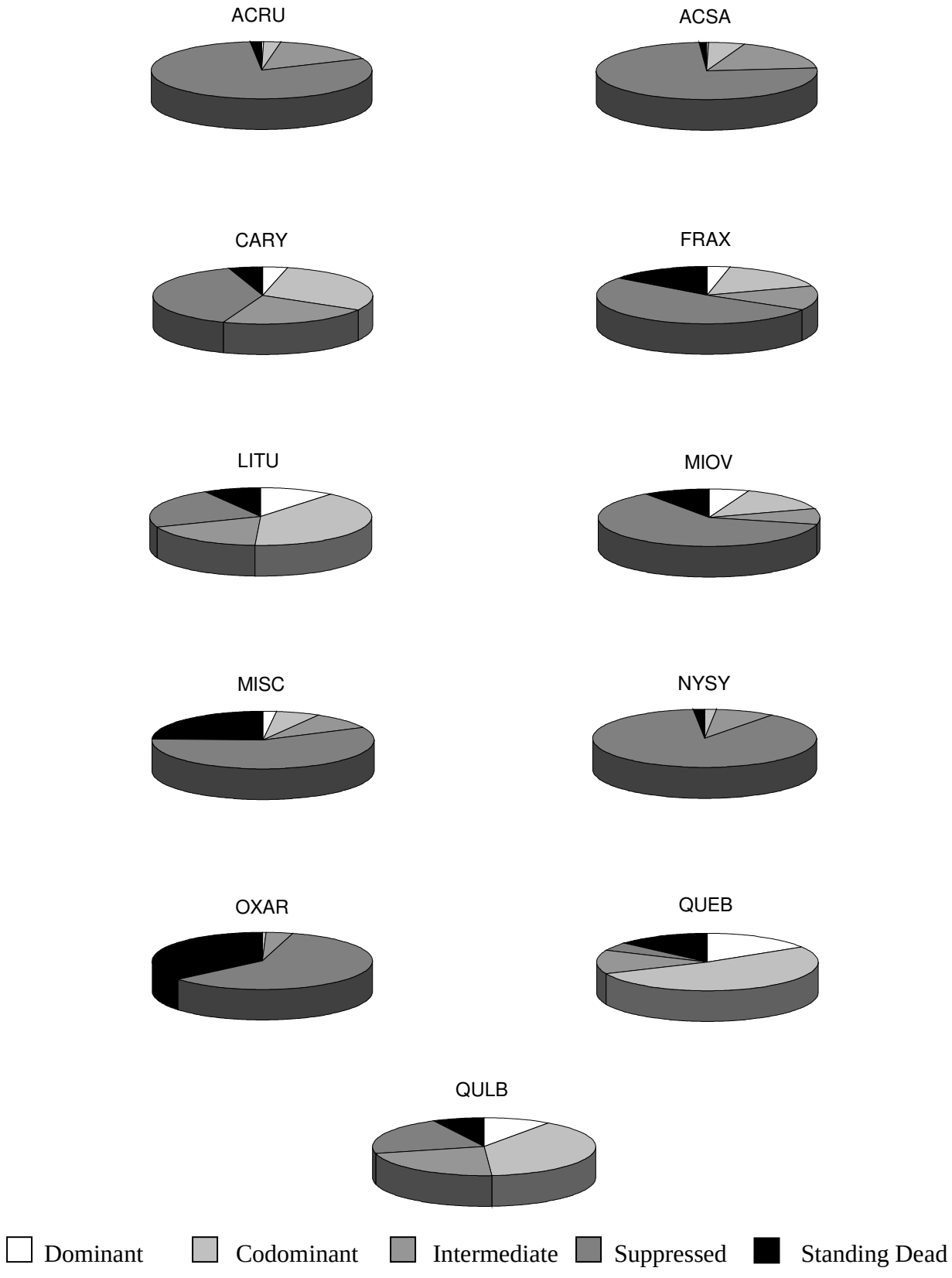

Figure 2.—The relative abundance of trees in the five crown classes for the species groups defined in Table 5.

Branch Die Back

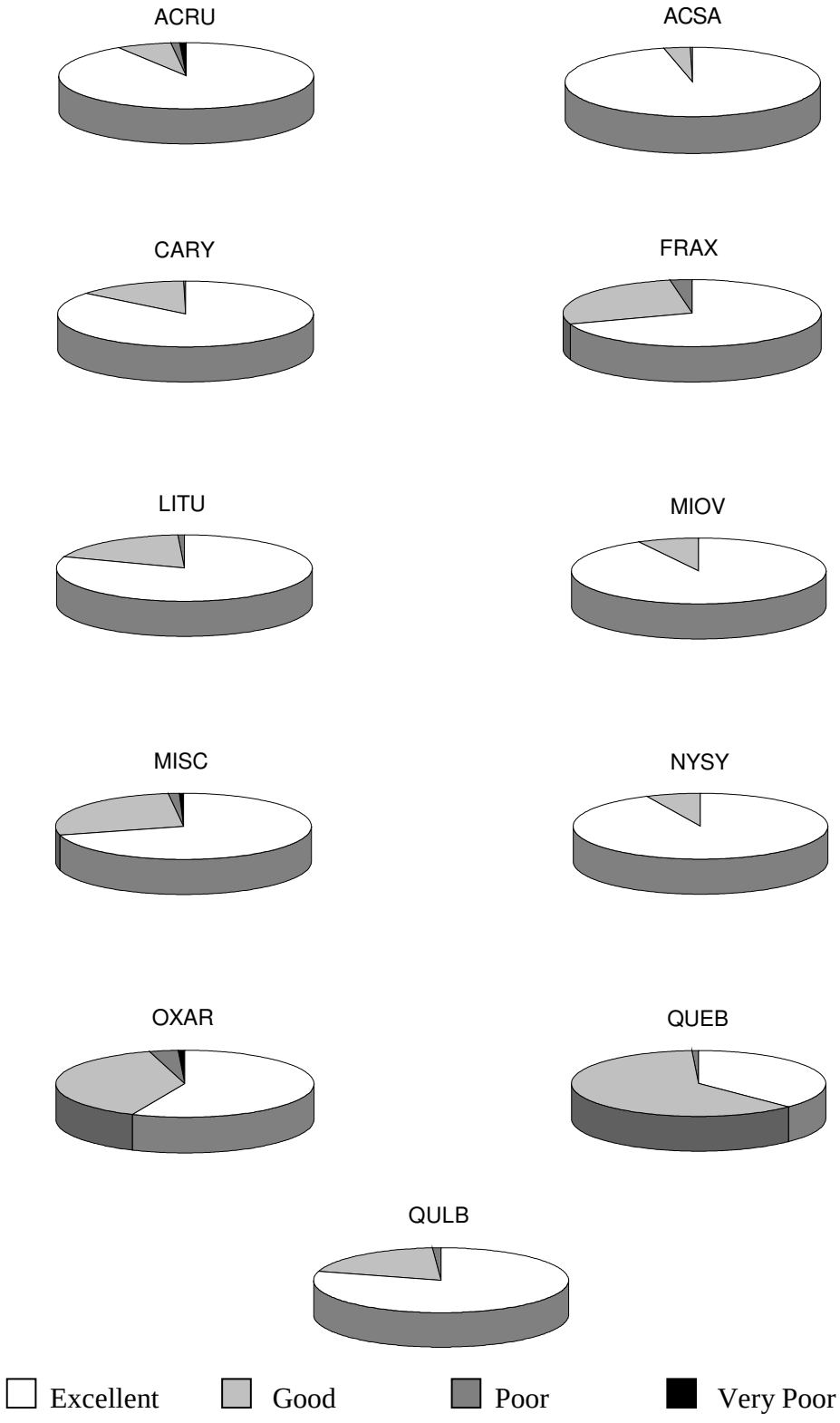

Figure 3.—The relative abundance of tree species groups (see Table 5) for classes of branch die-back. The classes are defined as excellent (<15%), good (15-44.9%), poor (45-74.9%), and very poor (>=75%).

Foliage Transparency

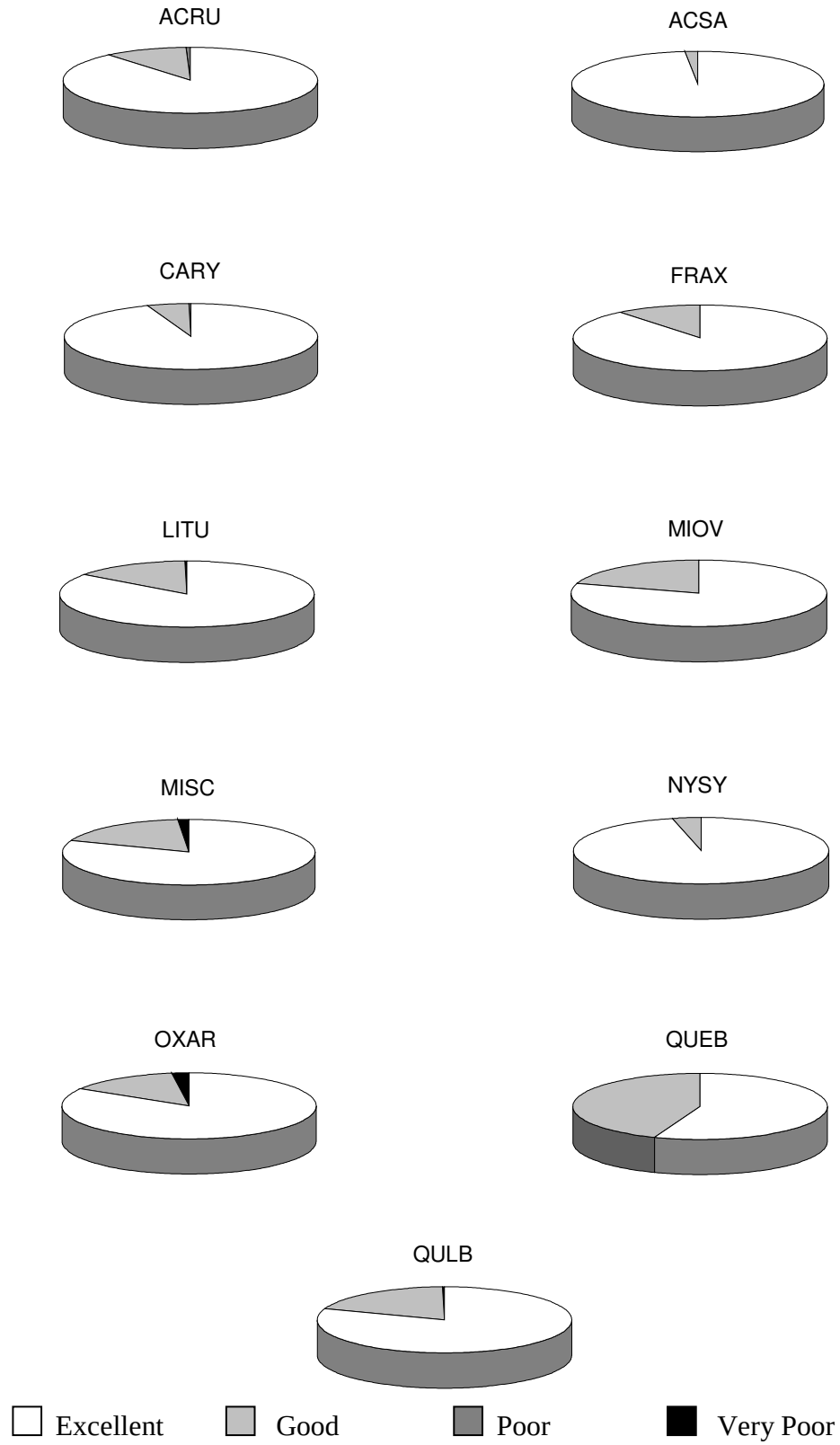

Figure 4.— The relative abundance of tree species groups (see Table 5) for four classes of foliage transparency. The classes are defined as excellent (<15%), good (15-44.9%), poor (45-74.9%), and very poor (>=75%).

Table 4.—Crown condition of overstory trees by size class.

Item	D.b.h. (cm) 10 to 24.9	25 to 39.9	40 +	Total
	———Percent———			*Percent*
Crown class				
Dominant	0.00	0.51	6.37	6.88
Codominant	0.69	16.19	10.83	27.71
Intermediate	9.82	7.44	0.36	17.61
Suppressed	38.06	1.11	0.04	39.20
Standing dead	8.13	0.34	0.13	8.60
Total	56.70	25.58	17.73	100.00
Total trees	3026	1365	946	5337
Foliage transparency (%)				
5	7.25	1.70	0.72	9.66
10	39.37	20.33	13.06	72.76
20	6.11	5.31	5.27	16.69
30	0.20	0.10	0.14	0.45
40	0.00	0.04	0.00	0.04
50	0.04	0.00	0.00	0.04
90	0.06	0.02	0.00	0.08
100	0.27	0.00	0.00	0.27
Total	53.31	27.50	19.19	100.00
Total trees	2609	1346	939	4894
Branch Dieback (%)				
5	12.28	1.96	0.57	14.81
10	32.61	18.47	11.73	62.81
20	6.11	6.23	5.95	18.29
30	1.12	0.69	0.88	2.70
40	0.37	0.06	0.02	0.45
50	0.39	0.06	0.02	0.47
60	0.06	0.00	0.02	0.08
70	0.14	0.00	0.00	0.14
80	0.12	0.00	0.00	0.12
90	0.10	0.02	0.00	0.12
Total	53.31	27.50	19.19	100.00
Total trees	2609	1346	939	4894

blackgum now are abundant in the smaller size classes (10 to 25 cm d.b.h.). Five tolerant species (dogwood [*Cornus florida*], red maple, sugar maple, blackgum, and beech) accounted for more than 80 percent of the stems in the sapling layer (1.4 m tall to 9.9 cm d.b.h.; Chapter 8). Although the age structures of these forests have not been determined, our results suggest that most of dominant and codominant oaks were established during the stand-initiation stage (Oliver and Larson 1996) in the mid- to late-1800s, and the size-class distributions suggest that shade-tolerant species have invaded these stands more recently. Similar trends of maple invasion in second-growth oak forests in the region have been documented (Tift and Fajvan 1999; Schuler and Fajvan 1999). The initiation of maple invasion during this period corresponds with sharp regional decreases in the frequency and spatial extent of fire (Yaussy and Sutherland 1994), suggesting a causal link. The decrease in fire frequency (ca. 1930) was caused at least in part by fire-suppression policies implemented in Ohio and across the Nation (Pyne 1982).

Although 50,000 acres of forest were defoliated by the gypsy moth (*Lymantria dispar*) in northeastern Ohio in 1996 (http://www.hcs.ohio-state.edu/ODNR/Health / gypsymoth.htm), the invasion front has not yet reached southeastern Ohio. The crown condition of these stands was good with respect to measures of foliage transparency and branch dieback (Millers et al. 1991). In similar oak-dominated forests in southwestern Pennsylvania, gypsy moth defoliation caused a 20- to 40- percent increase in mortality of overstory oaks, resulting in subsequent increases in the basal area of red and sugar maple (Fajvan and Wood 1996). The expanding gypsy moth front is projected to reach our study areas soon. In addition to the increasing abundance of maples and other shade-tolerant species at the four sites, gypsy moth defoliation likely will cause these successional trends to accelerate.

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Table 5.—Average density of overstory (≥ 10 cm d.b.h.) tree species present in 1995 in the four study areas (N=5106 live trees, 13.5 ha sampled, in 108 plots).

Scientific name	Common name	Study area[a]	Code[b]	No. live trees/ha	No. standing dead/ha
Acer rubrum	Red maple	A B W Y	ACRU	52.9	1.0
Acer saccharum	Sugar maple	A B W Y	ACSA	31.6	0.4
Aesculus flava	Yellow buckeye	A B W Y	MIOV[c]	1.9	0.0
Amelanchier arborea	Downy serviceberry	A Y	MISC[d]	0.2	0.1
Carpinus caroliniana	American hornbeam	W	MISC	0.1	0.0
Carya spp.	Hickory	A B W Y	CARY	37.0	1.9
Cercis canadensis	Eastern redbud	A B Y	MISC	0.6	0.0
Cornus florida	Flowering dogwood	A B W Y	MISC	4.0	1.3
Fagus grandifolia	American beech	A B W Y	MIOV	6.0	0.1
Fraxinus spp.	Ash	A B W Y	FRAX	8.3	1.3
Ilex opaca	American holly	W	MISC	0.1	0.0
Juglans nigra	Black walnut	A B W	MIOV	0.5	0.0
Liriodendron tulipifera	Yellow-poplar	A B W Y	LITU	20.7	1.9
Nyssa sylvatica	Blackgum	A B W Y	NYSY	17.0	1.3
Ostrya virginiana	Eastern hophornbeam	B	MISC	0.1	0.0
Oxydendrum arboreum	Sourwood	A B W Y	OXAR	10.0	5.0
Pinus echinata	Shortleaf pine	B	MIOV	0.5	0.7
Pinus virginiana	Virginia pine	B	MIOV	0.1	0.1
Platanus occidentalis	Sycamore	B	MIOV	0.1	0.0
Populus grandidentata	Bigtooth aspen	A W Y	MIOV	0.1	0.3
Quercus alba	White oak	A B W Y	QULB[e]	79.0	7.4
Quercus coccinea	Scarlet oak	A B W Y	QUEB[f]	11.8	2.3
Quercus prinus	Chestnut oak	A B W Y	QULB	49.2	2.6
Quercus rubra	Northern red oak	A B W Y	QUEB	13.4	1.5
Quercus velutina	Black oak	A B W Y	QUEB	24.0	3.7
Sassafras albidum	Sassafras	A B W Y	MIOV	2.1	2.1
Tilia americana	American basswood	A W Y	MIOV	4.4	0.0
Tsuga canadensis	Eastern hemlock	A	MIOV	0.1	0.0
Ulmus rubra	Slippery elm	A B W Y	MIOV	2.6	0.1

[a] Denotes presence of each species in four study areas: A = Arch rock, B = Bluegrass Ridge, W = Watch Rock, Y = Young's Branch.

[b] Codes assigned to species with more than 100 live trees (see Figs. 2-4).

[c] Species with potential to produce trees that will occupy the canopy.

[d] Species with no potential to produce trees that will occupy the canopy.

[e] White oak group (subgenus *Lepidobalanus*).

[f] Red oak group (subgenus *Erythrobalanus*).

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Chapter 10

Foliar Nutrient Concentrations of Oak, Hickory, and Red Maple

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Abstract

Early autumn foliar nutrient concentrations of overstory oak (white oak [*Quercus alba* L.] or chestnut oak [*Q. prinus* L.]) understory hickory (mockernut hickory [*Carya tomentosa* (Poir.) Nutt.] or pignut hickory [*C. glabra* (Mill.) Sweet]), and both overstory and understory red maple (*Acer rubrum* L.) were analyzed in relation to Integrated Moisture Index (IMI) classes. Foliar nutrient concentrations varied among the three species groups, emphasizing that differential uptake and utilization of nutrients is species dependent. Concentrations in late summer were within the range reported for these species for all nutrients except nitrogen (N). Concentrations of N were below the presumed normal range for oaks and hickory, likely due to the late sampling date. Leaves were collected in late September just as autumn coloration was beginning, indicating that retranslocation was occurring. Foliar nutrient concentrations in red maple did not differ between the Watch Rock and Arch Rock study areas, between designated treatment units (control and frequent burn), or between understory and overstory trees. Differences in concentrations between IMI classes were limited to the oaks and hickories. In hickory, foliar P and Mg increased significantly from the xeric to intermediate sites. However foliar P in oak was greatest in intermediate plots and lowest in mesic plots. These limited differences in concentrations between IMI classes did not always reflect differences in A-horizon soil chemistry [TIN (total inorganic nitrogen), PO_4, Ca, Mg, Al] indicating that factors in addition to soil concentrations play a role in nutrient uptake.

Introduction

Nutrient availability is a key site component affecting the productivity of natural ecosystems. It is determined by numerous factors, including those that influence the soil's ability to supply nutrients as well as the plants' ability to utilize them (Corey and Schulte 1973; Jungk 1996). Such factors include soil physical and chemical properties, soil microorganisms, water availability, plant species, and physical and chemical properties of plant roots, including mycorrhizal infection (Corey and Schulte 1973; Grigal 1990; Bledsoe and Atkinson 1991; Chapin 1991). Foliar nutrient concentrations reflect the combined influence of these many factors, and provide a means of evaluating sites for deficiencies or monitoring potential changes due to natural and anthropogenic disturbances and management practices (Mitchell 1936; Leaf 1973).

Most of the elements essential to plant growth are assimilated through root absorption of ions from the soil solution (Jungk 1996). Thus, water availability is an important determinant of nutrient availability and can greatly affect plant growth. As soil water content decreases, transpiration is reduced and ions become less mobile (Walker 1991). This reduces nutrient availability and can occur even before reductions in soil water potential restrict water uptake for most plants (Nye and Tinker 1977). Both topographic and edaphic characteristics are important in determining the available soil moisture of a site (Fralish 1994; Meiners et al. 1984). Single indexes such as the Integrated Moisture Index (IMI) have been developed to integrate topographic and soil features of the landscape that affect moisture levels in forest ecosystems (Iverson et al. 1997; Chapter 3). The IMI classification can then be related statistically to ecological processes.

Mixed-oak forests of southern Ohio, like many other eastern forests, are becoming dominated by red maple in the understory and midstory in part because red maple exhibits growth and physiological characteristics of both early and late successional species and tends to have lower water, nutrient, and light requirements than other species (Abrams 1998). We were interested in determining how foliar nutrient concentrations varied among species

exhibiting different growth characteristics within the mixed-oak forests of southern Ohio. Species typically found on all plots were selected for study and included overstory white and chestnut oak, (longlived, intermediate shade tolerance), understory pignut and mockernut hickory (sapling size, intermediate shade tolerance) and red maple (shortlived, fastgrowing, shade intolerant) (Burns and Honkala 1990). We were also interested in determining whether tree size or crown position within the canopy affects foliar nutrient concentrations. Red maple was one of the few species that was commonly found as both understory and overstory trees on these plots. Thus, the purpose of this study was: (1) characterize the foliar nutrient chemistry of overstory oak, understory hickory and overstory and understory red maple growing in southern Ohio, and (2) determine whether soil moisture and soil chemistry affect foliar nutrient chemistry.

Methods

Study Areas and Experimental Design

The study areas and experimental design are described in detail in Chapter 1. Here a brief overview is provided. The four 75-90 ha study areas are located in Vinton County (Arch Rock and Watch Rock) and Lawrence County (Young's Branch and Bluegrass Ridge). The study areas are within in the Southern Unglaciated Allegheny Plateau, which is characterized by high hills, sharp ridges, and narrow valleys. Sandstones and shales are principle bedrocks. Forests are oak-dominated and the current overstory originated in the late-1800s, after the cessation of clearcutting for the charcoal iron industry.

In each study area, three prescribed fire treatments were established, a control unit (CONT), an infrequent burn unit (INFR), and a frequent burn unit (FREQ). To account for variation in soil moisture and vegetation, a GIS-derived integrated moisture index (IMI) was applied across the dissected landscapes of the study areas (Chapter 3). From the calculated IMI scores, each 30 x 30 m pixel was assigned to one of three soil moisture classes: xeric, intermediate, or mesic. Thus to examine the effects of prescribed fire and account for environmental heterogeneity, a split-plot experimental design was established. The four study areas are replicate blocks, fire treatment units are whole plots, and IMI classes are subplots. The 50 x 25 m vegetation plots (N= 108 total) were established as pseudoreplicates in each IMI class within each fire treatment unit (Chapter 1).

Field and Laboratory Methods

On September 25-27, 1995, foliage samples were collected from randomly selected healthy understory and overstory trees from the xeric, intermediate, and some mesic plots for the Cont and Freq units at WR and AR. Leaves were collected from two dominant or codominant overstory red maples and three understory red maples within or near the plots. At WR additional foliage was sampled from two overstory oak (white or chestnut oak), and three understory hickory (mockernut or pignut hickory) in or near each plot. Overstory trees had a dbh >10 cm and understory trees had a dbh of 3-10 cm. Approximately 25 oak and red maple leaves and approximately 3 hickory leaves were collected from the outer portion of the mid to upper third of the canopy of each sampled tree using pole pruners or by shooting down the foliage. Fewer hickory leaves were collected due to the larger size of the compound leaf and the limited number of leaves per tree. The general condition of the leaves was noted at the time of collection.

Leaf samples were dried for 48 h at 70°C and ground prior to analysis. In the laboratory, total kjeldahl nitrogen (N) and total phosphorus (P) in a kjeldahl digest were determined for each tree using a Lachat Autoanalyzer (Diamond 1992). Concentrations of K, Ca, Mg, Mn, Fe, Cu, Zn, B, Al, and Na were analyzed by dry ashing the sample, dissolving the ash in nitric acid and analyzing the solution by inductively coupled plasma emission spectrophotometry (Watson 1981) at the Research Extension Analytical Laboratory at the Ohio Agricultural Research and Development Center, Wooster, OH.

Data Analysis

Overstory and understory red maple were common on all plots. However, the number and species of oaks and hickories varied from plot to plot. There were hickories on the mesic sites (Table 1). Because of this uneven tree distribution, data are presented as species groups (oaks, hickories, red maple overstory or understory) rather than as individual species.

Differences among treatment units and IMI classes were determined with a mixed model ANOVA (Littell et al. 1996) using plot means followed by single degree-of-freedom contrasts when significant differences were detected. Data from each species group were analyzed separately. Additional analyses were run to determine differences among study areas and canopy position in red maple, and to compare foliar nutrient concentrations among the three species groups. All analyses were run using SAS version 6.12 (SAS 1990).

Results

Macronutrients

Foliar nutrient concentrations of the five macronutrients differed significantly among the three species (Table 2). There were no significant differences between the overstory

Table 1. - Number of plots and total number of trees of each species[1] sampled at Watch Rock and Arch Rock study areas.

Study area	Treatment unit	IMI classification	Number of plots	Overstory			Understory		
				RM	WO	CO	RM	PH	MH
Watch Rock	C	Xeric	3	6	0	6	9	6	3
		Intermediate	2	4	4	0	6	4	0
		Mesic	1	2	0	2	3	0	0
	F	Xeric	2	4	0	4	6	1	5
		Intermediate	4	8	5	3	12	4	8
		Mesic	0	0	0	0	0	0	0
Arch Rock[2]	C	Xeric	3	6	—	—	9	—	—
		Intermediate	1	2	—	—	3	—	—
		Mesic	2	4	—	—	6	—	—
	F	Xeric	4	8	—	—	12	—	—
		Intermediate	2	4	—	—	6	—	—
		Mesic	0	0	—	—	0	—	—

[1]RM=red maple, WO=white oak, CO=chestnut oak, PH=pignut hickory, MH=mockernut hickory.
[2]Only overstory and understory red maple were sampled at Arch Rock

and understory red maple, so the maple data were combined for this analysis. Foliar N and P were significantly greater in the oaks compared to both the hickories and red maple, which exhibited similar concentrations. Oak and hickory had similar concentrations of K, which in turn were significantly greater than those of red maple. Levels of Ca and Mg were greatest in hickory while those in maple and oak were similar.

Concentrations of N, K, Ca, and Mg oak foliage did not differ significantly between the Cont and Freq units or among IMI classes (Appendix). However, P was significantly higher in the Cont unit, and intermediate IMI plots had greater concentrations of P than the xeric or mesic plots. For hickory, P and Mg were greatest in the intermediate plots (Appendix). A significant treatment-by-IMI class interaction was present such that foliar P was considerably lower in hickories from the Freq unit than from the Cont unit on the xeric plots, yet there were no differences between treatment units (Appendix).

Red maple growing at WR and AR had similar foliar macronutrient concentrations; there were no significant differences in nutrient concentrations due to designated treatment unit or IMI class. (Appendix). Likewise, crown position had no apparent effect on macronutrient concentrations of red maple. (Appendix).

Trace Elements

Trace Element concentrations tended to be higher in hickory foliage than in oak or red maple foliage except for Cu, which was highest in maple (Appendix). Although the magnitude of differences in foliar concentrations between species was generally zero to fivefold, concentrations of Al were 80 to 150 times higher in hickory, than in oak or red oak.

Foliar concentrations of the trace elements in oaks and hickories differed between treatment units and among IMI classes. Significant differences due to treatment unit, IMI or their interactions were detected in the oaks for Mn, Fe, Cu, Zn, and Na. (Appendix). Interactions generally resulted from a difference in the direction of the response to soil moisture in the Cont and Freq units. Hickory also showed differences in Mn and B concentrations. There were differences in concentrations of trace elements in red maple between treatment units or among IMI classes. (Appendix). However, there were differences in these concentrations in overstory red maple foliage between study areas. Overstory red maple at WR had higher concentrations of Mn ($p = 0.0165$), Fe ($p = 0.0030$), Zn ($p = 0.0130$), and Al ($p = 0.0001$), and lower concentrations of Na (0.0046) than at AR. Similar differences were not present in the understory red maple.

Discussion

Late summer foliar nutrient concentrations of P, K, Ca, and Mg in oak were within the range reported for white and chestnut oak, but N concentrations tended to be lower than values reported in other studies (Mitchell 1936; Leaf 1973; Boerner 1984; Jones et al. 1991). Limited data were available for hickory, but N values were below those reported for mockernut hickory (Abrams and Mostoller 1995) and hickory species in general (Kaczmarek et al. 1998; Martin et

Table 2. - Analysis of Variance probabilities of significant differences due to treatment unit, IMI class and their interaction.

Species/Source	Numer-ator d.f.	Denom-inator d.f.	Macronutrient p-values				
			N	P	K	Ca	Mg
Overstory Oak[1]							
Treatment unit	1	7	0.1177	0.0169	0.3477	0.5160	0.9900
IMI class	2	7	0.5469	0.0429	0.3213	0.5609	0.5302
Treatment*IMI	1	7	0.9734	0.1095	0.8786	0.0765	0.9253
Understory Hickory[1]							
Treatment unit	1	7	0.6053	0.1536	0.0553	0.1070	0.2175
IMI class	1	7	0.0940	0.0311	0.4520	0.5247	0.0134
Treatment*IMI	1	7	0.1967	0.0448	0.4300	0.3464	0.6175
Overstory Red Maple[2]							
Treatment unit	1	1	0.9023	0.4247	0.7068	0.4431	0.6544
IMI class	2	3	0.2728	0.6205	0.1011	0.2942	0.6086
Treatment*IMI	1	3	0.3320	0.3158	0.2283	0.0848	0.0451
Understory Red Maple[2]							
Treatment unit	1	1	0.4234	0.5152	0.5961	0.5485	0.8291
IMI class	2	3	0.1487	0.5986	0.6527	0.5941	0.8766
Treatment*IMI	1	3	0.5322	0.2639	0.8848	0.2867	0.9838

[1] Analysis includes trees from Watch Rock study area only.

[2] Analysis includes trees from Watch Rock and Arch Rock study areas.

al. 1998). Macronutrients in both overstory and understory red maple were within the ranges reported for this species (Mitchell 1936; Boerner 1984; Jones et al. 1991; Abrams 1998). Trace element concentrations for all species fell within the ranges reported by Leaf (1973) for forest trees.

The low concentrations of N in oak and hickory foliage might have been related to sampling time. Since concentrations can vary considerably throughout a growing season, the timing of sampling is critical. Deciduous foliage should be sampled after full leaf expansion but before appreciable redistribution of nutrients in late summer or autumn (Walker 1991). The retranslocation of nutrients from deciduous foliage to stems occurs 3 to 4 weeks prior to leaf abscission (van den Driessch 1984). Our samples were collected just as leaf coloration was visible beginning in some trees though only green leaves were collected for analyses. However, translocation of mobile nutrients (N, P, K, Mg) was most likely occurring, resulting in foliar concentrations lower than expected. Alternatively, foliar nitrogen may have reflected low soil nutrient availability on these acidic soils though this seems unlikely since soil data suggest that these sites are becoming N-enriched and may no longer be nitrogen limited (Chapter 5). Soil Ca/Al (mole/mole) ratios below 1.0 were common at AR and WR, particularly in xeric plots (Chapter 5). This suggests the possible increased risk of adverse impacts on tree growth and nutrition due to Al stress and greater nutrient imbalances (Cronan and Grigal 1995).

Inherent differences among species play an important role in the absorption and utilization of mineral nutrients from the soil (Goddard and Hollis 1984). This can result in differences in foliar nutrient concentrations and in the allocation of minerals within a tree. As expected, oak, hickory, and red maple growing in close proximity demonstrated differences in foliar nutrient concentrations. Lower concentrations of N, P, and K in red maple relative to oak in mixed oak forests have been reported (Mitchell 1936; Boerner 1984; Martin et al. 1998). Red maple generally has lower nutrient requirements than many tree species in the Eastern United States (Abrams 1998).

Tree size and crown class can affect the anatomy, morphology, and ecophysiology of leaves within a forest canopy due to the uneven distribution of light (Leaf 1973). For example, leaves grown at low irradiance

generally are thinner and have a lower leaf mass per area and N content than those grown at high irradiance (Abrams and Kubiske 1990; Abrams and Mostoller 1995). They also tend to have more chlorophyll on a leaf-weight basis, thus increasing light harvesting pigments as a way to maximize net CO_2 fixation at low irradiance (Boardman 1977). These changes can alter the partitioning of nutrients within the leaves. We found no significant differences in foliar nutrient concentrations (mg N g^{-1}) between overstory and understory red maple. Similarly, Abrams and Mostoller (1995) found no differences in N concentrations between open-grown and understory trees of six deciduous species, including red maple. They did find that the N content (g N m^{-2}) was significantly greater in open-grown plants for most species, and suggested that this reflects differential N partitioning. We will consider leaf concentrations and content in subsequent collections.

The A-horizon soils at AR and WR had similar chemical properties except for NH_4 and TIN (total inorganic nitrogen), which were both significantly greater at WR (Chapter 5). However, foliar N in overstory and understory trees was similar at both study areas and did not reflect this difference in soil nitrogen. Trace nutrients other than Al were not tested in the soils. Concentrations of trace elements in foliage from overstory red maple grown at AR differed significantly from those at WR, suggesting that actual soil concentrations or conditions that affect uptake differed at the two study areas.

Differences in foliar nutrient concentrations among xeric, intermediate, and mesic plots were limited to P in oak and hickory and Mg in hickory. This was surprising since water availability is an important factor in nutrient uptake (Jungk 1996) and there were significant differences in chemical properties of A-horizon soils among IMI classes. Soil concentrations of TIN, PO_4, Ca, and Mg generally were significantly lower in xeric than in intermediate and mesic plots, which did not differ significantly from each other (Chapter 5). By contrast Al decreased with increasing soil moisture. Foliar N, Ca, and Al did not show this same pattern for any tree species, but P in oak and hickory and Mg in hickory did increase from xeric to intermediate plots, demonstrating how soil chemistry is not always a good predictor of foliar chemistry. The decrease in P at mesic sites did not follow this pattern, but only one mesic plot was sampled and this may not reflect the general trend. Precipitation was not limiting during the spring and early summer when leaves were expanding, suggesting that sufficient moisture was available in the plots of all three IMI classes, and that initial nutrient uptake was not affected greatly on any of the plots. Variations in foliar nutrient levels may be more apparent during drier years when differences in soil moisture availability are more pronounced among xeric, intermediate, and mesic plots.

Our data provides a baseline for monitoring seasonal and yearly changes in foliar nutrient concentrations of oaks, hickory and red maple in southern Ohio, and in investigating the relationship between foliar and soil chemistry, and site conditions. Foliar nutrient dynamics will continue to be monitored to assess the short- and long-term effects of prescribed fire.

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Appendix — Trace element concentrations (mean+1 se) in foliar tissue collected in September 1995. Probabilities for differences due to treatment unit, IMI class, and treatment*IMI class interactions are presented.

Treatment/ IMI class	# plots	Trace Element (mg kg^{-1}) Mn	Fe	B	Cu	Zn	Al	Na
Overstory Oak								
Treatment C								
Xeric	3	880.7	48.16	50.96	5.89	15.66	74.83	12.22
		(3.6)	(3.27)	(4.39)	(0.20)	(0.67)	(1.15)	(0.76)
Intermediate	2	777.9	53.29	47.14	6.06	15.21	80.24	7.92
		(106.0)	(6.93)	(3.40)	(0.67)	(3.16)	(13.15)	(0.18)
Mesic	1	719.7	48.23	57.75	5.48	15.35	64.78	10.23
Treatment F								
Xeric	2	563.1	57.67	57.55	4.51	11.67	78.9	7.75
		(47.0)	(4.05)	(2.98)	(0.12)	(0.93)	(4.04)	(1.12)
Intermediate	4	658.0	48.24	54.24	5.80	12.77	69.66	11.97
		(28.8)	(1.39)	(5.69)	(0.16)	(0.94)	(1.90)	(1.65)
Overall Mean	12	716	50.68	53.50	5.60	13.80	73.89	10.38
		(28.1)	(1.55)	(1.95)	(0.15)	(0.56)	(2.14)	(0.61)
Source		Analysis of Variance Probabilities						
Treatment Unit		0.0004	0.4304	0.1503	0.0073	0.0202	0.4159	0.8599
IMI Class		0.2608	0.6300	0.4193	0.0294	0.9553	0.1958	0.9962
Treatment*IMI		0.0253	0.0295	0.9533	0.0384	0.4968	0.0930	0.0069
Understory Hickory								
Treatment C								
Xeric	3	654.9	65.92	68.05	6.70	99.10	5341	11.93
		(39.0)	(4.51)	(3.38)	(0.27)	(10.34)	(636)	(1.18)
Intermediate	2	632.5	62.94	64.45	7.26	94.42	7551	11.14
		(16.6)	(8.77)	(0.44)	(0.60)	(16.42)	(1517)	(1.76)
Treatment F								
Xeric	2	544.0	59.13	75.6	6.51	105.96	4723	10.73
		(25.0)	(1.85)	(0.27)	(0.30)	(7.44)	(385)	(0.28)
Intermediate	4	771.8	66.30	72.08	7.49	92.16	6055	11.74
		(42.2)	(1.18)	(1.86)	(0.58)	(10.02)	(996)	(0.75)
Overall Mean	12	678.8	64.13	71.01	7.05	96.86	5836	11.47
		(31.8)	(1.86)	(1.89)	(0.21)	(4.62)	(402)	(0.40)
Source		Analysis of Variance Probabilities						
Treatment Unit		0.6887	0.6167	0.0066	0.9744	0.8152	0.2443	0.7384
IMI Class		0.0196	0.5429	0.1155	0.1231	0.3621	0.0707	0.9052
Treatment*IMI		0.0079	0.1655	0.9919	0.6522	0.6455	0.6144	0.3388

Appendix cont.

Treatment/ IMI class	# plots	Trace Element (mg kg^{-1}) Mn	Fe	B	Cu	Zn	Al	Na
Overstory Red Maple								
			Watch Rock Study Site					
Treatment C								
Xeric	3	802.2	44.58	36.71	9.60	27.58	50.57	6.44
		(44.3)	(2.07)	(0.58)	(1.09)	(1.40)	(7.91)	(1.33)
Intermediate	2	734.0	49.71	38.77	10.57	29.87	50.45	6.40
		(7.2)	(2.93)	(4.03)	(0.74)	(4.10)	(17.08)	(0.37)
Mesic	1	760.6	53.08	38.54	12.35	24.68	54.23	3.76
Treatment F								
Xeric	2	475.7	49.88	45.40	6.83	21.05	56.31	5.34
		(31.3)	(1.44)	(8.86)	(1.14)	(3.96)	(8.97)	(0.27)
Intermediate	4	620.2	41.24	40.44	8.59	19.96	49.24	8.47
		(56.6)	(2.06)	(3.90)	(0.61)	(0.81)	(3.48)	(1.24)
			Arch Rock Study Area					
Treatment C								
Xeric	3	566.2	39.02	36.85	9.31	17.65	41.68	7.43
		(60.8)	(3.44)	(2.66)	(1.53)	(2.61)	(2.18)	(1.03)
Intermediate	1	520.6	29.06	40.66	8.02	17.46	21.66	7.36
Mesic	2	489.2	32.56	36.35	10.54	17.16	32.30	8.92
		(42.4)	(0.24)	(1.29)	(0.18)	(1.09)	(1.67)	(0.16)
Treatment F								
Xeric	4	639.2	55.38	39.43	9.53	21.85	38.44	8.23
		(29.35)	(6.05)	(2.08)	(0.79)	(1.82)	(2.48)	(1.13)
Intermediate	2	683.8	35.16	40.50	8.50	27.32	28.68	9.96
		(22.0)	(5.40)	(1.74)	(0.92)	(0.77)	(0.84)	(1.50)
Overall Mean	24	632.9	43.92	39.22	9.27	22.32	43.29	7.53
		(19.37)	(1.58)	(0.95)	(0.34)	(0.84)	(1.96)	(0.41)
Source			Analysis of Variance Probabilities					
Treatment Unit		0.7297	0.4860	0.4106	0.3882	0.7684	0.7994	0.3815
IMI Class		0.6906	0.2006	0.8985	0.4105	0.4284	0.2896	0.4682
Treatment*IMI		0.1090	0.1081	0.4646	0.8244	0.9186	0.9498	0.2638

Appendix cont.

Treatment/ IMI class	# plots	Trace Element (mg kg^{-1}) Mn	Fe	B	Cu	Zn	Al	Na
Understory Red Maple								
			Watch Rock Study Site					
Treatment C								
Xeric	3	741.5	44.76	36.68	6.61	20.46	41.52	5.41
		(40.)	(4.24)	(2.12)	(0.42)	(2.96)	(5.36)	(0.76)
Intermediate	2	723.6	40.02	31.74	8.13	28.87	35.97	8.01
		(52.3)	(2.77)	(2.70)	(0.48)	(2.32)	(12.29)	(2.29)
Mesic	1	646.5	45.19	35.49	8.05	33.23	26.54	7.48
Treatment F								
Xeric	2	518.1	44.50	37.88	6.51	21.5	43.92	4.78
		(9.2)	(5.88)	(1.55)	(1.60)	(1.15)	(4.16)	(1.34)
Intermediate	4	657.7	40.39	30.76	6.46	23.52	35.84	6.25
		(71.3)	(2.46)	(1.13)	(0.71)	(1.81)	(0.92)	(0.71)
			Arch Rock Study Area					
Treatment C								
Xeric	3	551.9	37.36	37.20	7.87	18.42	36.44	9.18
		(38.04)	(1.69)	(6.59)	(0.16)	(2.47)	(1.13)	(1.83)
Intermediate	1	532.1	28.40	31.55	6.90	14.12	27.14	8.82
		(-)	(-)	(-)	(-)	(-)	(-)	(-)
Mesic	2	485.8	35.11	35.16	7.90	17.56	29.74	6.58
		(57.0)	(0.06)	(1.75)	(0.42)	(2.00)	(1.50)	(0.67)
Treatment F								
Xeric	4	655.0	63.04	33.20	8.43	26.52	47.10	10.25
		(50.3)	(13.00)	(2.82)	(0.76)	(3.47)	(10.40)	(0.99)
Intermediate	2	647.4	46.10	39.66	8.38	28.10	31.53	9.92
		(73.5)	(11.70)	(2.51)	(1.22)	(3.60)	(3.17)	(1.46)
Overall Mean	24	622.0	44.34	34.64	7.52	23.41	37.64	7.76
		(16.6)	(1.87)	(0.88)	(0.22)	(0.90)	(1.94)	(0.37)
Source		Analysis of Variance Probabilities						
Treatment Unit		0.9049	0.2921	0.9830	0.9132	0.4766	0.4950	0.9560
IMI Class		0.4567	0.3257	0.4819	0.9023	0.4579	0.1720	0.4929
Treatment*IMI		0.4561	0.4415	0.4258	0.4111	0.6184	0.5429	0.4879

Chapter 11

Monitoring Selected Arthropods

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Abstract

Arthropod populations were sampled in four study areas in southern Ohio in 1995 to document patterns of arthropod diversity and establish a baseline dataset for long-term monitoring in mixed-oak forests. Pitfall, Malaise, and blacklight traps were operated in 12 treatment units from May through September. Several insect groups were selected for detailed study due to their abundance and potential to reflect community dynamics. These taxa include ground beetles (Family: Carabidae), scarab beetles (Family: Scarabaeidae), long-horned beetles (Family: Cerambycidae), carrion beetles (Family: Silphidae), syrphid flies (Family: Syrphidae), ants (Family: Formicidae), vespid wasps (Family: Vespidae), and nocturnal moths (Order: Lepidoptera). From these 8 groups, a total of 706 species were identified, but only 15 species were relatively abundant and evenly distributed across all treatment units. In addition to these common species, several rare species were collected. This work has added to a growing database documenting forest arthropod diversity in southern Ohio.

Introduction

Few studies have attempted to document arthropod diversity across several taxonomic groups within a single ecosystem (Dunwiddie 1991; Parsons et al. 1991; Lattin 1993). Although an all-taxa biodiversity inventory was recently initiated in the Great Smoky Mountains National Park, such studies are rare due to the immense diversity of arthropods. With limited resources, it is nearly impossible to adequately sample all arthropods in a community considering the time, labor, funding, and taxonomic expertise necessary to accomplish such a task. To further complicate matters, arthropod samples often contain many scarce species whose presence provides little information about community dynamics.

Our research efforts concentrated on a limited number of taxa based on their potential to provide information on the long-term dynamics of arthropod communities. These selected groups are common, easily collected, and readily identified insect taxa whose biology is relatively well known. Each of these groups also is associated with the forest floor, and thus are more likely to be affected by surface fires than canopy-dwelling arthropods. Prescribed fire might affect microclimatic conditions on the forest floor by increasing soil temperature and/or decreasing soil moisture.

Among surface-inhabiting arthropods, ground beetles (Coleoptera: Carabidae) are commonly monitored to study the dynamics of community change. Ground beetles are important predators of phytophagous and fungivorous insects and populations are sensitive to changes in soil surface conditions. In past studies, these beetles have served as indicators of environmental disturbance (Basedow 1990; Mossakowski et al. 1990), historical land use (Pizzolotto and Brandmayr 1990), and ecological habitat type (Eyre and Luff 1990; Maelfait and Desender 1990). Sampling these beetles via pitfall traps provides reliable estimates of populations based on their activity on the forest floor (den Boer 1985). Fluctuations in abundance and the absence or presence of certain species can provide information on environmental trends (Thiele 1977).

The scarab beetle subfamilies Scarabaeinae and Geotrupinae (Coleoptera: Scarabaeidae) also are closely associated with the soil surface and are common in southern Ohio. Most Scarabaeinae and Geotrupinae adults are dung feeders, though some species prefer fungus and carrion (Howden 1955). Wind, temperature, and humidity on the forest floor strongly affect the microhabitat of dung (biologically and physically) which in turn can affect the fecundity of these beetles (Helgesen 1967).

Another large beetle family commonly found in Ohio's deciduous forests is the long-horned beetles (Coleoptera: Cerambycidae). Most larvae in this family bore through wood and many are destructive to trees and freshly cut logs (Borrer et al. 1989). Increases in long-horned beetle populations can be indicative of increased environmental stress on nearby trees and/or an increase in the amount of dead timber.

Carrion beetles (Coleoptera: Silphidae) are not a major component of the forest floor community but are important as scavengers and are readily sampled by pitfall trapping. We paid special attention to this family in an attempt to document remaining populations of the federally endangered American burying beetle (*Nicrophorus americanus*), last reported from Ohio in a neighboring county in 1974.

In addition to beetles, several insect families also are common and readily sampled in southern Ohio forests. Ants (Hymenoptera: Formicidae) are typically the most numerous arthropods in most terrestrial ecosystems and are closely associated with soil and/or standing and downed timber. Many flies and wasps are easily collected by Malaise trapping and can be useful measures of forest floor conditions. Examples include syrphid flies (Diptera: Syrphidae) and vespid wasps (Hymenoptera: Vespidae). Some syrphids depend on nectar sources and soil surface moisture and, therefore, could be useful in assessing surface conditions. Vespid species that nest in decaying wood may also reflect surface conditions.

Due to the high diversity of moths and butterflies (Lepidoptera), there have been few studies that have comprehensively sample the lepidopteran fauna of deciduous forests (e.g. Butler et al. 1995; Teraguchi and Lublin 1999). However, many lepidopteran species could be important in assessing community changes. Larvae that feed in leaf litter or on low-growing lichens and shrubs are more likely to be affected by environmental changes to the forest floor than species whose larvae feed in tree canopies. Most nocturnal lepidopterans (primarily moths) are easily sampled with blacklight traps; however, species with a relatively short flight range are better indicators of local environmental conditions (Opler and Buckett 1970).

Our research is a component of a large-scale ecosystem management study of prescribed fire in mixed-oak forest ecosystems. Our objective was to document patterns of arthropod abundance and diversity in selected taxonomic groups to establish an adequate baseline for evaluating the effects of prescribed fire.

Methods

Study Areas and Experimental Design

The study areas and experimental design are described in detail in Chapter 1. Here a brief overview is provided. The four 75-90 ha study areas are located in Vinton County (Arch Rock and Watch Rock) and Lawrence County (Young's Branch and Bluegrass Ridge). The study areas are within in the Southern Unglaciated Allegheny Plateau, which is characterized by high hills, sharp ridges, and narrow valleys. Sandstones and shales are principle bedrocks. Forests are oak-dominated and the current overstory originated in the late-1800s, after the cessation of clearcutting for the charcoal iron industry. In each study area, three prescribed fire treatments were established, a control unit (CONT), an infrequent burn unit (INFR), and a frequent burn unit (FREQ).

Field Methods

In 1995, arthropod traps were deployed near the center of each treatment unit in each of the four study areas. Traps were located at or near ridgetops near the center of the treatment units to reduce edge effects.

Pitfall trapping

In each treatment unit we installed a linear transect of twelve plastic pitfall traps (11-cm diam.) positioned approximately 10 m apart. Each trap was buried with the lip flush with the soil surface and contained 150 ml of ethylene glycol as a killing agent and preservative. A rain cover and mammal-resistant screen were installed over each trap. Traps were in place from May 10 to September 28 (Vinton County) and May 11 to October 10 (Lawrence County). Samples were retrieved and ethylene glycol replaced at weekly intervals until September, thereafter biweekly. All ground beetles (Carabidae), scarab beetles (Scarabaeidae), carrion beetles (Silphidae), and ants (Formicidae) were separated and preserved in 70 percent ethanol for identification to species. Remaining arthropods were preserved in ethanol for future identification.

Malaise trapping

One standard Townes-type Malaise trap (Townes 1962) fitted with custom wet collecting heads was installed in each treatment unit between May 10 and June 1. The collecting head concentrated specimens into an ethanol-filled jar, which was changed weekly. Traps were in place until September 28 at the Vinton County areas and October 10 at the Lawrence County areas. Contents of collecting jars were sorted and the following insect families were identified to species: long-horned beetles

Table 1.—Number of species in selected insect families trapped at study areas in 1995 (numbers in parentheses are number of species unique to the study area).

Family	Study Area[a] AR	BR	WR	YB
Coleoptera:				
Carabidae[b,c]	72(10)	50(2)	64(5)	73(7)
Scarabaeidae[b]	18(0)	15(1)	18(0)	15(0)
Cerambycidae[c,d]	33(5)	29(2)	45(9)	29(5)
Silphidae[c]	6(0)	6(0)	8(0)	6(0)
Diptera:				
Syrphidae[d]	25(4)	15(1)	23(3)	20(3)
Lepidoptera:				
Arctiidae[d]	23(0)	26(2)	24(1)	25(3)
Noctuidae[c]	159(6)	156(19)	184(21)	162(20)
Notodontidae[c]	21(1)	25(3)	31(4)	25(1)
Saturniidae[c]	7(0)	8(2)	9(0)	10(0)
Sphingidae[c]	10(1)	8(2)	9(0)	10(0)

[a] - AR = Arch Rock, Vinton Furnace Experimental Forest, Vinton Township, Vinton County, Ohio. BR = Bluegrass Ridge, Wayne National Forest, Aid Township, Lawrence County, Ohio. WR = Watch Rock, Vinton Furnace Experimental Forest, Vinton Township, Vinton County, Ohio. YB = Young's Branch, Wayne National Forest, Decatur Township, Lawrence County, Ohio.
[b] – species collected by pitfall traps
[c] – species collected by light traps
[d] – species collected by Malaise traps

(Cerambycidae), syrphid flies (Syrphidae), ichneumon wasps (Ichneumonidae), social wasps (Vespidae), and selected Lepidoptera. Horse flies and deer flies (Tabanidae) and tachina flies (Tachinidae) also were separated but not identified to species. The remaining arthropods were preserved in ethanol for future study.

Light-trap sampling

In each treatment unit, a BioQuip bucket-type light trap with an 8-watt fluorescent ultraviolet lamp and 12-volt timer was operated from 9 p.m. until 5 a.m. one night per week from May to September; there were 13 trap-nights at AR and WR and 10 trap-nights at BR and YB. A 2.5-liter bucket hung beneath each light containing ethyl acetate vapor and dichlorvos-impregnated strips as killing agents. Bucket contents were removed the following day, placed in plastic bags, and then stored in a freezer for later identification.

Results

Arthropod taxa collected by the three trapping techniques included spiders (Araneae), harvestmen (Opiliones), mites and ticks (Acari), pillbugs (Isopoda), millipedes (Diplopoda), centipedes (Chilopoda), and insects (Insecta). Of these arthropods, only selected insect families in the orders Coleoptera (beetles), Diptera (true flies), Hymenoptera (ants, bees, and wasps), and Lepidoptera (butterflies and moths) were identified to species (Appendices 1 and 2).

Beetles (Coleoptera)

Ninety-eight species of ground beetles (Carabidae) were collected (Appendix 1). Carabid richness per study area ranged from 50 at BR to 73 at YB (Table 1). Pitfall sampling collected more than 5,100 carabids representing 45 species. However, only 7 species were captured in all 12 treatment units. Fifty-nine carabid species were collected from the light-trap samples, with 13 occurring in all four study areas. Only 7 species were collected by both trapping methods, indicating that the two techniques sample different members of this important family. Of all species, only *Galerita bicolor, Pterostichus tristis*, and *Synuchus impunctatus* were common and evenly distributed across all treatment units (Table 2). Pitfall and blacklight traps also captured *Carabus sylvosus, Piesmus submarginatus*, and *Cyclotrachelus incisus*, all previously unrecorded in Ohio (Purrington and Stanton 1996). *Carabus sylvosus* was fairly common in the Vinton County pitfall traps.

Twenty-one species of scarab beetles (Scarabaeidae) were identified from pitfall and light traps combined (Appendix 1). Although more than 40 percent of these species were observed at all four study areas, only *Ateuchus histeroides*, *Geotrupes splendidus*, and *Onthophagus striatulus* occurred abundantly and evenly in all study areas (Table 2). *Ateuchus histeroides* was the most abundant scarab species in all the pitfall samples and its abundance was significantly greater at the Vinton County sites than the Lawrence County sites. Among the Geotrupinae, the most abundant species was *Geotrupes splendidus*.

Sixty-two species of long-horned beetles (Cerambycidae) were collected by all three trap types combined (Appendix 1). Cerambycidae richness was greater at WR (45 species) than the other study areas (29-33 species; Table 1). Twelve species were collected at all four study areas but no single species was found in comparable numbers across all treatment units.

Table 2.—Mean abundance ± s.e. of 15 common insect species across study sites, 1995; means followed by the same letter are not significantly different at p=0.05 (one-way ANOVA); where no letters are shown, means are not significantly different.

	Study Area			
Insect Species	AR	BR	WR	YB
Coleoptera: Carabidae[a]				
Galerita bicolor	181±67.3	66±30	50±17	60.7±5.3
Pterostichus tristis	39.3±18.9	19±8.9	27±3	39.3±25.2
Synuchus impunctatus	256±155.3	27±9.5	215.7±47.1	75±9.7
Coleoptera: Scarabaeidae[a]				
Ateuchus histeroides	342±111.7[a]	73.7±39.6[b]	281±24.6[a]	37±20.2[b]
Geotrupes splendidus	34.3±2.3	13.7±4.1	50.7±18.7	17.3±4.3
Onthophagus striatulus	73±23.3	22.3±9.7	54.7±21.4	46±8.6
Coleoptera: Silphidae[a]				
Nicrophorus orbicollis	240.3±25.7	97.3±54.6	220±29.5	153.7±50.6
Diptera: Syrphidae[b]				
Volucella vesicularia	32±11.8	21.3±5.9	39.7±13.6	26.7±4.4
Hymenoptera: Formicidae[a]				
Aphaenogaster rudis rudis	366.3±95.5	451±136.2	357.3±26.9	305±52.9
Camponotus spp.	314.3±96.4	377±232.2	807.7±260	485.7±85.1
Lepidoptera: Saturniidae[c]				
Actias luna	24.7±6.6	11.3±1.3	23.7±3.3	18±4.5
Automeris io	40±7.5[a]	18±1.2[b]	24.7±5.2[ab]	38.7±2.7[a]
Dryocampa rubicunda	81±21	31.7±9.5	70±12.1	106±21.8
Lepidoptera: Satyridae[b]				
Cyllopsis gemma	71.7±32.7	31±5.9	72.3±44.1	20±7
Lepidoptera: Zygaenidae[b]				
Pyromorpha dimidiata	60.7±25.7	24.7±15.6	38.7±21.2	57.7±10.1

[a] specimens collected by pitfall traps
[b] specimens collected by Malaise traps
[c] specimens collected by blacklight trap

Eight species of carrion beetles (Silphidae) were identified, of which the burying beetle *Nicrophorus orbicollis* was most abundant, accounting for 92 percent of all Silphidae collected (Appendix 1). This species was common on all study sites and analysis of variance (ANOVA) revealed no statistically significant differences in numbers within or between areas (Table 2). No *Nicrophorus americanus* were recovered.

Incidental observations during this study included several rare beetles. Two specimens of *Megalopinus caelatus* (Staphylinidae) were collected at BR; no previous records are known from Ohio. *Anelaphus pumilum* (Cerambycidae), collected at WR, may be the first collection in Ohio (T. K. Philips, Western Kentucky University, pers. commun.). The first record of *Pemelus costatus* (Hydrophilidae) in Ohio was collected in pitfall traps near WR and BR (M. Archangelsky, CRILAR, Argentina, pers. commun.). *Onthophilus pleurocostatus*, a hister beetle collected in a baited pitfall trap, was new record for Ohio (P. Kovarik, Ohio State University, pers. commun.). *Platydema erythrocerum* (Tenebrionidae), collected in a blacklight trap at WR, was also previously unrecorded in Ohio (C.A. Triplehorn, pers.commun.).

Table 3.—Mean abundance ± s.e. of common insect families captured by Malaise traps 1 June - 22 Sept. 1995. Means followed by the same letter are not significantly different at p=0.05 (one-way ANOVA); where no letters are shown, means are not significantly different.

	Study Area			
Insect family	AR	BR	WR	YB
Diptera:				
Syrphidae	31±11.5	21.3±6	39.7±17	26.7±4.4
Tabanidae	547.7±316.6[a]	205.3±58.3[b]	250.3±92.8[b]	564.7±81.3[a]
Tachinidae	71.7±1	50.3±4.4	77.7±22.9	42.3±5.5
Hymenoptera:				
Ichneumonidae	767.3±134.3[a]	293.3±48.7[b]	353.7±100[b]	362.7±32.9[b]

True Flies (Diptera)

Thirty-seven species of syrphid flies (Syrphidae) were identified from Malaise trap samples (Appendix 1). Nine species were collected at all study areas, but only *Volucella vesicularia* was common and evenly distributed (Table 2). Syrphid flies were not as abundant as horseflies and deer flies (Tabanidae) or tachina flies (Tachinidae). There were significant differences in the abundance of tabanids (Tabanidae) among study areas with significantly higher numbers at AR and YB than BR and WR. The abundance of tachinids was evenly distributed across study areas (Table 3).

Ants and Wasps (Hymenoptera)

Eight species of ants (Formicidae) were recorded from all four study areas (Appendix 1). The most abundant species (Table 2) were in the genera *Aphaenogaster* and *Camponotus* (carpenter ants). Six species of social wasps (Vespidae) were identified but were neither abundant nor evenly distributed (Appendix 1). As a family, the ichneumon wasps (Ichneumonidae) were abundant at all four areas, with significantly greater numbers at AR than the other three study areas (Table 3).

Butterflies and Moths (Lepidoptera)

A total of 464 species in 26 families of macrolepidoptera were identified (Appendix 2). Fifty-three percent of these species were found at all four study areas. The most diverse family was the Noctuidae, of which WR had the highest richness, at 184 species (Table 1). Despite this diversity, only four moth species [*Actias luna* (Saturniidae), *Automeris io* (Saturniidae), *Dryocampa rubicunda* (Saturniidae), and *Pyromorpha dimidiata* (Zygaenidae)] and one butterfly [*Cyllopsis gemma* (Satyridae)] were abundant and evenly distributed across study areas (Table 2). Of these five species, only *Automeris io* showed any significant differences among study areas (Table 2).

Two clearwing moths (Sessiidae) collected by light trap were new records for Ohio (Purrington and Horn 1996). *Synanthedon acerni* was collected at all four study areas. *Synanthedon scitula* was collected only at AR.

Discussion

Overall carabid abundance collected via pitfall trapping was greater than that found in similar studies (Liebherr and Mahar 1979; Lenski 1982; MacLean and Usis 1992). However, the other studies contained fewer study sites and used periodic, rather than continuous, sampling. Likewise, carabid richness collected in these Ohio oak forests was greater than in other studies of similar habitat (Liebherr and Mahar 1979; Lenski 1982). Despite this diversity, many species only occurred in one study area. Only three species were abundant across all treatment units; these species should be important in the future as indicators of environmental change.

Unlike the carabids, species of scarab and silphid beetles were usually found in more than one study area. Species of long-horned beetles were often found in only one study area, though it is possible that more species were present in several study areas but not collected because Malaise and light trapping are not the standard method for collecting these beetles. Of these three families, only four species fit our criteria as potential indicators of environmental change.

The families Syrphidae, Tabanidae, and Tachinidae were abundant at all study areas, but the syrphid flies hold the most promise in assessing population shifts following prescribed fire due to their dependence on nectar sources and soil surface moisture. Within this family, only one species (*Volucella visicularia*) was abundant and evenly-distributed.

Of the hymenoptera, the carpenter ants (*Camponotus*) could be the most useful measure of forest floor surface conditions because they nest in decaying wood. However, their abundance in pitfall traps was determined primarily by the proximity of nests, and thus was highly variable. Therefore *Camponotus* may not be a reliable measure for comparing units or areas.

Many lepidopteran species were found at all study areas. However, many species in the diverse family Noctuidae were collected in only one study area . Of the many species collected, only five were sufficiently abundant and widely distributed to be considered potential indicators.

From these initial patterns of selected insect diversity, it is possible to identify abundant and evenly distributed species to assess the impact of altered microhabitat conditions following prescribed fire. For detecting changes in individual species, fifteen species hold the most promise as environmental indicators following prescribed fire. To detect changes in overall community composition, multivariate analyses (e.g., detrended correspondence analysis) can be used. Also, the species richness values reported here will be important for detecting changes in insect diversity following prescribed fires.

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Appendix 1-- Insect species in selected families recovered from study sites during 1995. p = pitfall trap; m = Malaise trap; l = light trap; o = observed on site; species newly recorded for Ohio are marked with *.**

Species	Study Area AR	BR	WR	YB
ORDER COLEOPTERA				
Carabidae[a]				
Agonum aeruginosum	1		1	
Agonum fidele			1	
Agonum harrisii	1			
Agonum placidum				p
Agonum punctiforme			1	p
Amphasia sericea			1	1
Anatrichis minuta				1
Anisodactylus carbonarius				1
Apenes lucidulus	p	p	1p	1p
Apenes sinuatus	1			1
Badister maculatus			1	1
Badister ocularis				1
Bembidion affine	1		1	1
Bembidion rapidum	1		1	1
Brachinus americanus			p	
Bradycellus tantillus	1			
Calathus gregarius	p			
Calathus opaculus	p		p	1
Calleida viridipennis	1	1	1	1
Calosoma wilcoxi	1			
Carabus goryi	p	p	p	p
*Carabus sylvosus****		p		p
Chlaenius emarginatus	1p	p	1p	p
Chlaenius tricolor	1		1	1
Cicindela sexguttata	mo	o	o	o
Cicindela unipunctata	p			
Clivina americana	1			1
Clivina bipustulata	1	1	1	1
Clivina dentipes	1			1
Clivina impressefrons				1
Coptodera aerata		1	1	1
Cyclotrachelus convivus	p	p	p	p
Cyclotrachelus freitagi			p	
*Cyclotrachelus incisus****	p		p	
Cymindis americanus	p	p	p	p
Cymindis limbatus	1p	1	1	1p
Cymindis neglectus	p		p	
Cymindis platicollis		1	1p	1
Dicaelus ambiguus	p		p	p
Dicaelus dilatatus		p		p
Dicaelus elongatus	p		p	p
Dicaelus furvus		p		
Dicaelus politus	p	p	p	p
Dicaelus purpuratus	p	p	p	p
Dicaelus teter	p	p	p	p

Species	Study Area AR	BR	WR	YB
Dromius piceus	1	1	1	1
Elaphropus sp	1			1
Galerita bicolor	1p	p	p	p
Galerita janus	p	p	p	
Harpalus compar		1	1	1
Harpalus erythropus	1		1	1
Harpalus pensylvanicus				1
Lebia analis				1
Lebia atriventris	1			1
Lebia fuscata	1		1	1
Lebia grandis		1	1	1
Lebia ornata				
Lebia pulchella	1			
Lebia solea	1	1		1
Lebia tricolor	1	1	1	1
Lebia viridipennis	1	1		1
Lebia viridis	1	1	1	1
Loxandrus velocipes		1	1	1
Loxandrus vitiosus	1		1	1
Myas coracinus	p	p	p	p
Notiobia terminata	1	1	1	1
Notiophilus aeneus	p	p	p	p
Oodes amaroides	1		1	1
Pasimachus punctulatus	p		p	p
Patrobus longicornis			1	
Pentagonica picticornis		1		1
*Piesmus submarginatus****	p			p
Platynus cincticollis	1			1
Platynus tenuicollis	1	1	1	1
Plochionus timidus	1	1	1	1
Poecilus chalcites			1	
Pterostichus adoxus	p	p	p	p
Pterostichus atratus	p	p		p
Pterostichus lachrymosus	p			
Pterostichus moestus	p			
Pterostichus permundus			p	
Pterostichus relictus	p		p	p
Pterostichus sayanus	p	p		
Pterostichus stygicus	p	p		
Pterostichus tristis	p	p	p	p
Rhadine caudata	p	p	p	p
Scaphinotus andrewsii mutabilis	p	p		p
Scaphinotus unicolor heros	p			
Selenophorus hylacis	1		1	1
Selenophorus opalinus	1	1	1	1
Sphaeroderus stenostomus lecontei	p	p	p	p
Stenolophus comma		1	1	

Appendix 1 cont.

Species	Study Area AR	BR	WR	YB
Stenolophus lecontei	1	1	1	1
Stenolophus ochropezus	1	1	1	1
Synuchus impunctatus	p	p	p	p
Trichotichus autumnalis		p	p	p
Trichotichnus dichrous	1	1	1	1
Trichotichnus vulpeculus	1	1	1	1
Zuphium americanum	1			
Scarabaeidae[c]				
Ateuchus histeroides	1p	1p	1p	1p
Canthon chalcites	p		p	p
Canthon viridis	p		p	p
Cloeotus globosus	1	1		
Copris fricator	p		p	p
Copris minutus		1p	1p	1p
Dichelonyx elongata	1	1	1	1
Dichotomius carolinus	1		1	
Dynastes tityus		1		
Eucanthus lazarus	1p	1p	1p	1
Geotrupes balyi	p		p	
Geotrupes hornii	1p	p	p	
Geotrupes semiopacus		p	p	
Geotrupes splendidus	p	p	p	p
Onthophagus orpheus canadensis	p		p	
Onthophagus hecate	p	p	p	p
Onthophagus s. striatulus	1p	p	1p	p
Pelidnota punctata	1	1	1	1
Phileurus valgus	1	1	1	1
Popillia japonica	o	o	o	o
Valgus canaliculatus		1	1	1
Xyloryctes jamaicensis	1p			p
Cerambycidae[b]				
Aegoschema modesta			m	1
Amniscus macula	1m	m	m	
Anelaphus pumilus				1
Analeptura lineola	m	m	m	
Aneflomorpha subpubescens	m	m	m	m
Astyleiopus variegatus		m		
Bellamira scalaris	m	m		
Brachyleptura rubrica				m
Clytus ruricola		m		m
Cyrtophorus verrucosus	m			
Distenia undata	m	m		
Eburia quadrigeminata			m	m
Ecyrus dasycerus	1m		1m	

Species	Study Area AR	BR	WR	YB
Elaphidion mucronatum		m	m	m
Elaphidionoides asperses	m	m	m	m
Elaphidionoides parallelus			1	
Elaphidionoides villosus	1m	1m	1m	1m
Enaphalodes rufulus	1		1	1
Euderces picepes			m	m
Gaurotes cyanipennis	m	m	m	m
Goes debilis			m	m
Goes pulcher			1	
Goes pulverulentus			1m	1m
Goes tesselatus	m	1	1	
Goes tigrinus	1		1	1
Graphisurus fasciatus		m	1m	
Hesperophanes pubescens			1	
Heterachthes quadrimaculatus	1		m	
Hetoemis cinerea			1m	
Hyperplatys aspersa				m
Knulliana cincta	1		1	
Lepturges angulatus	m			
Lepturges confluens			1	
Mecas pergrata		m		
Metacmaeops vittata	m	m	m	m
Monochamus titillator			1	
Necydalis mellita	m			
Neoclytus acuminatus	m	m	m	m
Neoclytus mucronatus	m	m	m	
Oberea bimaculata			m	
Oberea ruficollis	m		m	m
Oberea tripunctata	m			m
Orthosoma brunneum	1m	1m	1	1m
Physocnemum violaceipenne			m	
Prionus laticollis	p			
Psyrassa unicolor			m	
Rhopalophora longipes				m
Saperda candida			1	
Saperda discoidea		1m	1m	
Saperda lateralis	m	m		m
Sarosesthes fulminans		m	m	
Smodicum cucujiforme	1			
Stenocorus cinnamopterus		1	1	
Strangalepta abbreviata	m		m	
Strangalia bicolor	m	m	m	m
Strangalia luteicornis	m	m	m	m
Strophiona nitens	m	m	m	m
Tylonotus bimaculatus				1
Typocerus lugubris	m	m	m	m

Appendix 1 cont.

Species	Study Area AR	BR	WR	YB
Typocerus velutinus	m	m	m	
Urgleptes querci		m	m	
Xylotrechus colonus	m	m	m	m
Silphidae[d]				
Necrodes surinamensis			1	1
Necrophila americana	1p	p	p	p
Nicrophorus orbicollis	1p	1p	1p	1p
Nicrophorus pustulatus	1	1	1p	1
Nicrophorus sayi	1p	1p	1p	1p
Nicrophorus tomentosus	p	p	p	p
Oiceoptoma inaequale			p	p
Oiceoptoma noveboracense	p		p	
ORDER DIPTERA				
Syrphidae[e]				
Ceriana abbreviata	m		m	
Chilosia pallipes				m
Chilosia dives	m	m	m	m
Chrysotoxum perplexum	m	m	m	m
Dasysyrphus amolopsus	m			
Didea fuscipes	m		m	
Epistrophe sp.	m	m		
Eristalis arbustorum		m		
Eristalis bastardi	m			
Eristalis flavipes	m		m	m
Eristalis obscurus	m	m	m	m
Ferdinandea dives	m	m	m	
Melanostoma obscurum			m	m
Merodon equestris				m
Mesogramma geminata	m		m	
Mesogramma marginata	m	m	m	m
Metasyrphus emarginatus	m			m
Milesia virginiensis	m	m	m	m
Myiolepta nigra		m		m
Myiolepta varipes			m	
Platycheirus peltitoides	m			
Rhingia nasica				m
Somula decora	m			m
Sphaerophoria scripta			m	
Sphecomyia vittata			m	
Sphegina sp.	m			
Spilomyia hamifera			m	m
Spilomyia longicornis	m		m	
Syrphus sp.	m	m	m	m
Temnostoma balyras	m		m	
Temnostoma trifa		m	m	
Toxomerus geminatus	m	m	m	m
Volucella vesicularia	m	m	m	m
Xanthogramma flavipes	m	m	m	m
Xylota chalybea		m		m
Xylota flavitibia	m		m	
Xylota pigra	m			m
ORDER HYMENOPTERA				
Formicidae[f]				
Aphaenogaster rudis rudis	p	p	p	p
Camponotus americanus	p	p	p	p
Camponotus ferrugineus	p	p	p	p
Camponotus pennsylvanicus	p	p	p	p
Camponotus subbarbatus	p	p	p	p
Crematogaster lineolata	p	p	p	p
Formica subsericea	p	p	p	p
Prenolepis imparis imparis	p	p	p	p
Vespidae[g]				
Dolichovespula maculata	m	m	m	m
Polistes metricus	m		m	
Vespa crabro			m	
Vespula germanica	m		m	m
Vespula maculifrons	m	m	m	m
Vespula squamosa	m	m	m	m

[a] Specific determinations by F. F. Purrington.
[b] Specific determinations by T. K. Philips, D. J. Horn, D. M. Osborne and P. Blades.
[c] Specific determinations by T. K. Philips, F. F. Purrington and A. E. Smith.
[d] Specific determinations by D. J. Horn, G. D. Keeney and F. F. Purrington.
[e] Tentative determinations by E. Johnson and D. J. Horn.
[f] Specific determinations by G. Coovert, W. D. Raby and C. Ranger.
[g] Specific determinations by D. J. Horn.

Appendix 2—Lepidopteran species recovered from study sites during 1995; m = Malaise trap; l = light trap; o = observed on site; species newly recorded for Ohio are marked with *.**

Species[a]	Study area AR	BR	WR	YB
Oecophoridae				
Antaeotrichia schlaegeri	l	l	l	l
Sesiidae				
*Synanthedon scitula****		l		
*Synanthedon acerni****	l	l	l	l
Cossidae				
Prionoxystus robiniae		l	l	l
Tortricidae				
Argyrotaenia alisellana		l		l
Hesperiidae				
Epargyreus clarus	o		o	
Thorybes pylades	m			
Erynnis brizo	m	m	m	m
Erynnis juvenalis	m	m	m	m
Erynnis horatius	m	m	m	m
Pholisora catullus	m			
Ancyloxipha numitor		m		
Thymelicus lineola			m	
Polites peckius	m	m	m	m
Poanes hobomok			m	
Papilionidae				
Papilio polyxenes	o		o	
Papilio glaucus	o	o	o	o
Papilio troilus	mo	m	mo	m
Eurytides marcellus		o	o	
Pieridae				
Pieris rapae	o	m	o	o
Anthocharis midea	o		o	
Colias philodice			o	
Lycaenidae				
Feniseca tarquinius	m		m	m
Satyrium calanus		m		
Calycopis cecrops	m	m	m	m
Incisalia henrici		o	o	
Glaucopsyche lygdamus		m		
Everes comyntas	m	m	m	m
Celastrina ladon	mo	mo	mo	mo
Nymphalidae				
Polygonia interrogationis	o		o	o

Species	Study Area AR	BR	WR	YB
Polygonia comma			o	
Nymphalis antiopa	o		o	
Vanessa atalanta	o	o	o	o
Speyeria cybele	mo	m	o	
Chlosyne nycteis			o	
Phyciodes tharos	o	m	mo	m
Limenitis astyanax	mo	m	mo	
Satyridae				
Enodia portlandia	m		l	
Cyllopsis gemma	m	m	m	m
Hermeuptychia sosybius		m		
Megisto cymela	mo	m	m	m
Cercyonis pegala	m	m	lm	
Zygaenidae				
Pyromorpha dimidiata	m	lm	m	m
Megalopygidae				
Lagoa crispata	l	l	l	l
Norape ovina		l	l	l
Limacodidae				
Apoda yinversum	l	l	l	l
Apoda biguttata	l	l	l	l
Prolimacodes badia	l	l	l	l
Natada nasoni			l	
Euclea delphinii	l	l	l	l
Parasa chloris	l	l	l	l
Pyralidae				
Ostrinia nubilalis	l	l	l	l
Desmia funeralis	l	l	l	l
Palipita magniferalis	l	l	l	l
Pantographa limata	l	l	l	l
Euzophera ostricolorata		l		
Thyatiridae				
Habrosyne scripta	l			
Pseudothyatira cymatophoroides	l	l	l	l
Drepanidae				
Drepana arcuata	l		l	l
Oreta rosea	l	l	l	l

Appendix 2 cont.

Species[a]	Study area AR	BR	WR	YB
Geometridae				
Itame pustularia	l	l	l	l
Semiothisa promiscuata	l	l	l	l
Semiothisa granitata	l	l	l	l
Semiothisa quadrinotaria	l	l	l	l
Glena cribrataria		l	l	l
Iridopsis larvaria	l	l	l	l
Anavitrinella pampinaria	l	l	l	l
Epemecis hortaria	l	l	l	l
Melanolophia canadaria		l		l
Melanolopohia signataria	l	l	l	l
Biston betularia	l	l	l	l
Hypagirtis unipuncta	l	l	l	l
Lomographa vestaliata	l		l	
Lytrosis unitaria	l	l	l	l
Euchlaena amoenaria	l		l	l
Euchlaena tigrinaria	l	l	l	l
Euchlaena irraria	l	l	l	l
Nacophora quernaria	l	l	l	l
Campaea perlata	l	l	l	l
Metarranthis hypochraria				l
Probole nyssaria			l	l
Probole amicaria	l	l	l	l
Plagodis serinaria	l		l	l
Plagodis kuetzingi	l	l	l	l
Plagodis phlogosaria	l	l	l	l
Plagodis alcoolaria	l	l	l	l
Plagodis fervidaria	l	l	l	l
Besma endopriaria	l		l	
Besma quercivoraria	l	l	l	l
Tetracis crocallata	l	l	l	l
Tetracis cachexiata	l	l	l	l
Prochoerodes transversata			l	l
Nematocampa limbata	l		l	l
Nemoria bistriaria	l	l	l	l
Nemoria mimosaria	l	l	l	l
Dichorda iridaria	l	l	l	l
Cyclophora packardi	l		l	l
Scopula limboundata	l	l	l	l
Eulithis diversilineata	l	l	l	l
Ecliptopera atricolorata	l		l	l
Hydriomena transfigurata	l	l	l	l
Hydria prunivorata	l	l	l	l
Orthonama obstipata	l	l	l	l
Orthonama centrostrigaria	l	l	l	l
Eubaphe mendica	l	l	l	l
Eupithecia miserulata	l	l	l	l
Dyspteris abortivaria	l	l	l	l

Species	Study Area AR	BR	WR	YB
Mimallonidae				
Lacosoma chiridota		l		l
Cicinnus melsheimeri	l	l	l	l
Apatelodidae				
Apatelodes torrefacta	l	l	l	l
Olceclostera angelica	l	l	l	l
Lasiocampidae				
Malacosoma disstria	l	l	l	l
Malacosoma americanum	l	l	l	l
Saturniidae				
Eacles imperialis	l	l	l	l
Citheronia regalis	l	l	l	l
Citheronia sepulcralis		l		
Sphingicampa bisecta			l	l
Dryocampa rubicunda	l	l	l	l
Anisota stigma	l	l	l	l
Anisota virginiensis		l	l	
Automeris io	l	l	l	l
Antheraea polmphemus	l	l	l	l
Actias luna	l	l	l	l
Callosamia promethea		l		l
Callosamia angulifera	l	l	l	l
Sphingidae				
Manduca jasminearum		l		
Dolba hyloeus		l		
Ceratomia undulosa	l	l	l	l
Lapara coniferarum		l	l	
Smerinthus jamaicensis			l	
Paonias excaecatus	l	l	l	l
Paonias myops		l	l	l
Laothoe juglandis	lm	m	lm	m
Amphion floridana		m		
Pachysphinx modesta	l		l	
Sphecodina abbottii		l		l
Deidamia inscripta	l	l	l	l
Darapsa myron		l	l	l
Darapsa pholus	l	l	l	
Notodontidae				
Clostera albosigma			l	l
Clostera inclusa	l	l	l	l
Datana ministra		l		l
Datana angusii	l	l	l	l
Datana drexelii	l	l	l	l
Datana major		l		l

Appendix 2 cont.

Species[a]	Study area AR	BR	WR	YB
Datana contracta	1	1	1	1
Datana integerrima		1	1	
Nadata gibbosa	1	1	1	1
Hyperaeschra georgica	1	1	1	1
Peridea basitriens	1	1	1	1
Peridea angulosa	1	1	1	1
Pheosia rimosa	1		1	
Odontosia elegans	1		1	
Nerice bidentata		1		1
Ellida caniplaga	1	1	1	1
Gluphisia septentrionis			1	1
Furcula borealis				1
Furcula cinerea			1	
Symmerista albifrons	1	1	1	1
Dasylophia anguina	1	1	1	1
Dasylophia thyatiroides	1		1	1
Misogada unicolor		1		
Marcrurocampa marthesia	1	1	1	1
Heterocampa obliqua	1	1	1	1
Heterocampa subrotata	1			
Heterocampa umbrata	1	1	1	1
Heterocampa guttivitta	1	1	1	1
Heterocampa biundata		1	1	1
Lochmaeus manteo		1	1	1
Lochmaeus bilineata	1	1	1	1
Schizura ipomoeae	1	1	1	1
Schizura unicornis			1	
Schizura concinna			1	
Schizura leptinoides		1	1	1
Oligocentria semirufescens		1	1	
Oligocentria lignicolor	1	1	1	1
Hyparpax aurora				1
Arctiidae				
Crambidia pallida	1	1		1
Crambidia uniformis	1	1	1	1
Crambidia cephalica		1		1
Cisthene plumbea	1	1	1	1
Cisthene packardii		1	1	
Lycomorpha pholus	1		1	1
Hypoprepia miniata		1		
Hypoprepia fucosa	1	1	1	1
Clemensia albata	1	1	1	1
Pagara simplex				1
Haploa clymene	1	1	1	1
Haploa contigua	1	1	1	1
Haploa lecontei	1	1	1	1
Holomelina opella	1	1	1	1
Pyrrharctia isabella	1		1	1

Species	Study Area AR	BR	WR	YB
Estigmene acrea		1		
Spilosoma latipennis		1		1
Spilosoma congrua	1	1	1	1
Spilosoma virginica	1	1	1	
Hyphantria cunea	1	1	1	1
Ecpantheria scribonia	1	1	1	1
Apantesis phalerata			1	
Apantesis carlota				1
Grammia anna	1	1	1	1
Grammia figurata	1	1	1	1
Grammia parthenice	1	1	1	1
Grammia virgo				1
Halysidota tessellaris	1	1	1	1
Lophocampa caryae	1	1	1	1
Cycnia tenera	1	1	1	1
Euchaetis egle	1	1	1	1
Cisseps fulvicollis	1	1	1	1
Lymantriidae				
Dasychira tephra	1	1	1	1
Dasychira basiflava	1	1	1	1
Dasychira obliquata	1	1	1	1
Orgyia definita			1	1
Orgyia leucostigma	1	1	1	1
Noctuidae				
Idia americalis	1	1	1	1
Idia aemula	1	1	1	1
Idia majoralis				1
Idia rotundalis	1	1	1	1
Idia forbesi	1	1	1	1
Idia julia	1	1	1	
Idia diminuendis	1	1	1	1
Idia scobialis	1		1	1
Idia denticulalis		1		1
Idia lubricalis			1	1
Zanclognatha laevigata	1			
Zanclognatha obscuripennis		1		1
Zanclognatha pedipilalis			1	
Zanclognatha martha				1
Zanclognatha cruralis	1	1	1	1
Zanclognatha jacchusalis	1		1	
Zanclognatha ochreipennis		1	1	1
Chytolita morbidalis		1	1	
Macrochilo absorptalis			1	
Phalaenostola larentioides			1	
Tetanolita floridana				1
Bleptina caradrinalis	1	1	1	1
Renia salusalis		1	1	

Appendix 2 cont.

Species[a]	Study area AR	BR	WR	YB
Renia factioralis				1
Renia nemoralis				1
Renia discoloralis	1	1	1	1
Renia sobrialis		1	1	
Renia adspergillus		1		
Palthis angulalis	1	1	1	1
Palthis asopialis	1	1	1	1
Redectis vitrea		1		
Oxycilla malaca				1
Hypenodes fractilinea			1	
Dyspyralis puncticosta				1
Nigetia formosalis		1	1	
Bomolocha manalis	1	1	1	1
Bomolocha baltimoralis	1	1	1	1
Bomolocha bijugalis	1	1	1	1
Bomolocha palparia	1	1	1	1
Bomolocha abalienalis				1
Bomolocha deceptalis				1
Bomolocha madefactalis	1	1	1	1
Bomolocha sordidula				1
Plathmpena scabra	1	1	1	1
Spargaloma sexpunctata		1		
Pangrapta decoralis	1	1	1	1
Metalectra discalis		1	1	
Metalectra quadrisignata				1
Metalectra richardsi		1		
Arugisa latiorella		1		1
Scolecocampa liburna	1	1	1	1
Physopropus callitrichoides	1	1	1	1
Hypsoropha monilis		1		
Hypsoropha hormos	1	1	1	1
Scoliopteryx libatix				1
Calyptra canadensis	1	1	1	1
Panopoda rufimargo	1	1	1	1
Panopoda carneicosta	1	1	1	1
Cissusa spadix	1		1	
Lesmone detrahens		1		
Zale lunata	1	1	1	1
Zale galbanata	1		1	
Zale aeruginosa		1		
Zale undularis			1	
Zale minerea	1	1	1	1
Zale lunifera	1	1	1	1
Zale unilineata	1		1	
Zale horrida	1		1	1
Euparthenos nubilis	1	1	1	1
Allotria elonympha	1	1	1	1
Parallelia bistriaris	1	1	1	1
Euclidia cuspidea	1	1	1	

Species	Study Area AR	BR	WR	YB
Caenurgina erechtea	1	1	1	1
Mocis texana	1		1	1
Celipetra frustulum	1	1	1	1
Argyrostrotis anilis	1			1
Catocala piatrix	1			
Catocala habilis	1		1	1
Catocala robinsoni	1		1	
Catocala flebilis	1		1	1
Catocala angusi			1	1
Catocala obscura	1	1	1	1
Catocala retecta	1	1	1	1
Catocala residua	1	1	1	1
Catocala insolabilis	1			
Catocala vidua	1	1	1	1
Catocala paleogama	1	1	1	1
Catocala subnata	1		1	1
Catocala neogama	1	1	1	1
Catocala ilia	1	1	1	1
Catocala sordida		1		
Catocala andromedae	1	1	1	1
Catocala coccinata			1	1
Catocala miranda				1
Catocala ultronia	1	1	1	1
Catocala grynea		1		
Catocala dulciola		1		
Catocala clintoni			1	
Catocala similis	1	1		1
Catocala micronympha	1	1	1	1
Catocala amica	1	1	1	1
Catocala lineella	1		1	
Pseudoplusia includens	1	1	1	1
Allagrapha aerea		1	1	
Polychrisia morigera		1		
Chrysanympha formosa	1	1	1	1
Eosphoroptermx thyatiroides	1			1
Autographa precationis	1	1	1	
Anagrapha falcifera	1	1	1	1
Marathyssa inficita			1	
Paectes oculatrix	1	1	1	1
Paectes abrostollela	1	1	1	
Paectes abrostoliodes		1		
Eutelia pygmaea		1		
Eutelia pulcherrima	1			
Baileya ophthalmica	1	1	1	1
Baileya dormitans	1	1	1	1
Baileya levitans	1	1	1	
Baileya australis		1		
Characoma nilotica		1		
Meganola phylla	1	1	1	1

Appendix 2 cont.

Species[a]	Study area			
	AR	BR	WR	YB
Meganola spodia	1	1	1	1
Tripudia quadrifera			1	
Oruza albocostaliata	1	1	1	1
Hyperstrotia pervertens	1		1	1
Hyperstrotia villificans	1	1	1	1
Hyperstrotia secta	1	1	1	1
Thioptera nigrofimbria	1	1	1	1
Lithacodia muscosula	1	1	1	1
Lithacodia musta	1		1	1
Lithacodia carneola	1	1	1	1
Cerma cerintha	1	1	1	1
Leuconycta diphteroides	1	1	1	1
Leuconycta lepidula			1	
Tarachidia erastrioides			1	1
Panthea furcilla	1		1	
Colocasia flavicornis	1	1	1	1
Colocasia propinquilinea	1	1	1	1
Charadra deridens	1	1	1	1
Raphia frater	1	1	1	1
Acronicta americana	1	1	1	1
Acronicta dactylina	1		1	
Acronicta lepusculina				1
Acronicta betulae			1	
Acronicta radcliffei	1		1	
Acronicta funeralis	1	1	1	1
Acronicta vinnula	1	1	1	1
Acronicta superans				1
Acronicta laetifica		1	1	
Acronicta hasta	1	1	1	1
Acronicta spinigera	1	1	1	1
Acronicta morula	1	1	1	1
Acronicta interrupta		1	1	
Acronicta lobeliae	1	1	1	1
Acronicta heitzmani			1	1
Acronicta exilis			1	
Acronicta ovata	1	1	1	1
Acronicta modica	1	1	1	1
Acronicta haesitata	1	1	1	1
Acronicta tristis	1		1	
Acronicta hamamelis	1			
Acronicta increta	1	1	1	1
Acronicta inclara		1		
Acronicta retardata	1	1	1	1
Acronicta afflicta	1	1	1	1
Acronicta impleta	1	1	1	1
Acronicta lithospila	1	1	1	1
Acronicta oblinita		1		
Agriopodes fallax	1	1	1	1
Agriopodes teratophora		1	1	1

Species	Study Area			
	AR	BR	WR	YB
Polygrammate hebraeicum	1	1	1	1
Eudryas unio		1		1
Eudryas grata	1	1	1	1
Apamea cristata				1
Apamea vulgaris			1	
Apamea sordens				1
Agroperina helva			1	
Crymodes devastator				1
Oligia modica				1
Oligia fractilina	1			1
Oligia crytora	1			
Oligia semicana			1	
Oligia obtusa		1		
Archanara oblonga				1
Amphipoea velata				1
Bellura obliqua				1
Euplexia benesimilis	1	1	1	1
Phlogophora periculosa	1	1	1	1
Chytonix palliatricula	1	1	1	1
Dypterygia rozmani	1		1	
Phosphila turbulenta	1	1	1	1
Phosphila miselioides	1	1	1	1
Callopistria mollissima	1	1	1	1
Amphipyra pyramidoides	1	1	1	1
Anorthodes tarda	1	1	1	1
Balsa malana	1		1	
Balsa tristrigella	1	1	1	1
Balsa labecula	1	1	1	1
Elaphria versicolor	1	1	1	1
Elaphria festivoides	1	1	1	1
Elaphria grata		1		1
Galgula partita	1	1	1	1
Perigea xanthioides		1	1	
Platysenta videns	1	1	1	1
Ogdoconta cinereola			1	
Stiroides obtusa				1
Plagiomimicus pityochromus			1	
Basilodes pepita	1		1	1
Cosmia calami	1	1	1	1
Amolita fessa		1		
Lithophane petulca	1		1	
Lithophane hemina	1		1	
Lithophane antennata	1		1	
Pyreferra hesperidago			1	
Sideridis congermana			1	
Polia detracta	1	1	1	
Polia goodelli	1			1
Polia latex	1	1	1	1
Melanchra adjuncta	1	1	1	1

Appendix 2 cont.

Species[a]	Study area			
	AR	BR	WR	YB
Hadena ectypa			1	
Lacinipolia renigera	1	1	1	1
Lacinipolia lorea		1	1	1
Lacinipolia implicata	1	1	1	1
Pseudaletia unipuncta	1	1	1	
Leucania linda	1	1	1	1
Leucania ursula	1	1	1	1
Leucania pseudargyria	1	1	1	1
Orthosia rubescens	1			1
Crocigrapha normani	1		1	1
Egira alternans				1
Achatia distincta	1		1	1
Morrisonia confusa	1		1	
Nephelodes minians	1		1	1
Homorthodes furfurata	1	1	1	1
Ulolonche culea	1	1	1	1
Pseudorthodes vecors	1		1	
Orthodes crenulata	1	1	1	
Orthodes cynica	1	1	1	1
Tricholita signata			1	
Agrotis ipsilon	1	1	1	1
Feltia jaculifera	1	1	1	
Ochropleura plecta	1	1	1	1
Trichosilia geniculata		1		
Euagrotis illapsa	1			
Peridroma saucia	1	1	1	
Xestia adela	1		1	
Xestia dolosa	1	1	1	1
Xestia normaniana			1	
Xestia smithii	1		1	1
Xestia *bicarnea*	1		1	
Protolampra brunneicollis		1	1	
Abagrotis alternata		1	1	
Helicoverpa zea	1	1		1
Schinia arcigera	1		1	1

[a] - Specific determinations by E. H. Metzler, M. Gilligan, T. Gilligan, D. J. Horn, J. W. Peacock, R. D. Watkins and R. Zebold

Species sequence is standard from Hodges et al. (1983)

Chapter 12

Breeding Bird Communities

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Abstract

Prescribed burning is being applied on an experimental basis to restore and maintain mixed-oak communities in southern Ohio. This chapter describes baseline conditions for the breeding bird community prior to prescribed burning. We surveyed breeding bird populations at four study areas using the territory-mapping method. We observed 35 bird species during the surveys. The red-eyed vireo (*Vireo olivaceus*), ovenbird (*Seiurus aurocapillus*), wood thrush (*Hylocichla mustelina*), Acadian flycatcher (*Empidonax virescens*), and scarlet tanager (*Piranga olivacea*) were the most abundant, followed by the eastern wood-pewee (*Contopus virens*), hooded warbler (*Wilsonia citrina*), worm-eating warbler (*Helmitheros vermivorus*), and cerulean warbler (*Dendroica cerulea*). Densities of three bird species, the cerulean warbler, great crested flycatcher (*Myiarchus crinitus*), and eastern phoebe (*Sayornis phoebe*), varied among study areas. We compared our results to other surveys conducted in the Eastern United States and found that the composition of breeding bird communities was similar between mixed-oak and beech-maple forest types. We monitored 239 nests of 14 bird species to establish baseline levels of breeding productivity and to describe nest site selection. Predation of nest contents was the primary cause of nesting failure for most of the bird species monitored. Nest predation rates were highest for the ovenbird and wood thrush and lowest for the worm-eating warbler and Acadian flycatcher. Parasitism by brown-headed cowbirds (*Molothrus ater*) was a second factor limiting breeding productivity. Cowbird parasitism rates varied among host species but were comparable to rates reported from other studies. The overall nesting success rate for the wood thrush was lower than observed in other continuously forested landscapes in the Eastern United States, but this low rate was offset by the absence of cowbird parasitism for this bird species.

Introduction

Many species of forest birds in the eastern United States have declined in population (Sauer et al. 1997). The reasons for the declines are unclear, but possible explanations include loss of habitat, changes in habitat conditions, and increased fragmentation of remaining habitat (Finch 1991; Rappole and DeGraaf 1996). These changes underscore the need to monitor forest bird populations, document population trends, assess how these trends may be related to forest management activities, and identify habitat features that are important for maintaining population levels.

This chapter provides a general description of the breeding bird community inhabiting oak (*Quercus*)-dominated forests in southern Ohio. Oak-dominated forests are the most extensive forest type in the eastern United States (Powell et al. 1993), but forest inventories indicate that the proportion of forests dominated by oaks is declining (Griffith et al. 1993), as oaks are gradually being replaced by maples (*Acer* spp.) and beech (*Fagus grandifolia*). Prescribed burning is being applied on an experimental basis to assess its effectiveness in restoring and maintaining oak-dominated forests in the region. Effects of prescribed burning on various ecosystem components, including the breeding bird community, are being assessed by a long-term interdisciplinary research project (Chapter 1).

Many studies have shown changes in species composition or abundance of breeding bird communities in response to forest management practices (Thompson et al. 1996), including prescribed burning (Wilson et al. 1995; Salveter et al. 1996). Different bird species require specific structural features within the forest, such as large trees, dense understory vegetation, or thick leaf litter. These features provide critical nest sites or suitable foraging

areas. Forest management practices, such as prescribed burning, are likely to change the availability of these features and thus affect the community of forest birds.

Surveying bird populations is a standard procedure for describing and monitoring bird communities. Monitoring nesting productivity has become an additional standard approach to supplement surveys (Martin et al. 1997). Observations of active nests provide an indication of population health by assessing whether breeding productivity is sufficient to maintain existing populations or is so low that populations can be maintained only by immigration of individuals from surrounding areas (Van Horne 1983; Pulliam 1988). Nest predation is one of the primary factors affecting breeding productivity of forest birds. Selection of nest sites is likely to be nonrandom, based in part on the vulnerability of different sites to nest predators (Martin 1992). Identifying specific habitat features that directly affect reproductive success and assessing how the availability of these habitat features may change have become critical aspects of management plans that address conservation of breeding bird populations (Martin 1992). Thus, our goals in describing the baseline forest bird community were to: (1) estimate breeding bird population levels, (2) monitor nests of different bird species to estimate breeding productivity levels, (3) describe nest site selection and identify factors potentially influencing the likelihood of nesting success, and (4) compare our results to other published surveys to identify potential factors influencing the composition and breeding productivity of forest bird communities on a regional basis.

Methods

Study Areas and Experimental Design

The study areas and experimental design are described in detail in Chapter 1. Here a brief overview is provided. The four 75-90 ha study areas are located in Vinton County (Arch Rock and Watch Rock) and Lawrence County (Young's Branch and Bluegrass Ridge). The study areas are within in the Southern Unglaciated Allegheny Plateau, which is characterized by high hills, sharp ridges, and narrow valleys. Sandstones and shales are principle bedrocks. Forests are oak-dominated and the current overstory originated in the late-1800s, after the cessation of clearcutting for the charcoal iron industry. In each study area, three prescribed fire treatments were established, a control unit (CONT), an infrequent burn unit (INFR), and a frequent burn unit (FREQ).

Breeding Bird Populations

We used the territory-mapping method to estimate bird population densities (Robbins 1970). Each treatment unit was visited at least six times between mid-May and late June 1995. During each survey, locations of birds seen or heard were recorded on topographic maps. These observations were transferred to composite maps for each bird species and territories were delineated based on clusters of observations. To estimate bird densities, we counted the number of territories or bird pairs within each treatment unit and extrapolated to the number of territories per 40 ha. Densities were estimated only for bird species that occurred in discrete nonoverlapping territories smaller than the treatment units. Bird species were categorized by nest site and foraging site based on Ehrlich et al. (1988). Nest sites included ground, low shrub (less than 1 m), midstory (1 to 10 m), canopy (greater than 10 m), and rock. Foraging sites included ground, low shrub (less than 1 m), midstory (1 to 10 m), canopy (greater than 10 m), bole, and aerial. A one-way analysis of variance (ANOVA) was used to test for differences in bird densities (by species, nest site, foraging site, and total) among treatment units (Zar 1984).

We used IMI categories to describe the association of different bird species with moisture gradients. The IMI is based on solar radiation exposure, flow accumulation, soil water-holding capacity, and landscape curvature (Chapter 3). Three IMI categories are defined based on a continuum of values: xeric (IMI score less than 35), intermediate (35-50), and mesic (greater than 50). We assigned IMI categories to individual bird territories, and ran chi-square tests to compare observed and expected distributions of bird territories among IMI categories (Zar 1984). Expected distributions were calculated according to the existing composition of the four study areas combined (31 percent xeric, 40 percent intermediate, 29 percent mesic; Chapter 3).

To assess how typical the forest bird community observed at our study areas was relative to the general region, we compared our results with surveys conducted in deciduous forest habitat at 34 other sites in the Eastern United States. These survey results were compiled from primary literature and from a database of Breeding Bird Censuses compiled by the USGS Biological Resources Division (http://www.mp1-pwrc.usgs.gov/birds/ bbc.html). These surveys were conducted in mature forest habitat dominated by oak-hickory, beech-maple, or oak-pine (*Pinus* spp.). We converted survey results from densities or detection rates to percent composition by bird species within each site. We used detrended correspondence analysis (DCA) to compare the composition of the bird communities among the various sites (PC-ORD Version 3.05; McCune and Mefford 1997). DCA is an ordination technique that is appropriate for analyzing a sample-by-species abundance matrix (Gauch 1982). The result is a series of two-dimensional scores for each sample,

indicating similarities in overall species composition (Gauch 1982).

Nesting Success and Nest Site Selection

To assess levels of breeding productivity, we searched for and monitored active nests in each treatment unit between mid-May and late-July following standard protocol (Martin et al. 1997). Each treatment unit was marked with a 50-m grid of flagging to help relocate nests. Active nests were checked every 3 to 5 days to monitor their contents and determine their fate. We recorded fate as successful (nests that fledged at least one host young) or failed (nests that fledged no host young). We classified failed nests as depredated (nest, eggs, or nestlings disappeared), abandoned (eggs or nestlings left unattended in nest), or parasitized by brown-headed cowbirds (nest abandoned by host parents due to parasitism, or only cowbirds fledged successfully from nest).

Nesting success rates were estimated using the Mayfield method (Mayfield 1975), which calculates the daily nest survival rate (DSR), as follows:

$$DSR = 1 - \frac{\#\text{ of failed nests}}{\#\text{ of observation days}}$$

Observation days represent the pooled number of days that all active nests were observed, beginning with the first day of egg laying or the day an active nest was found, and ending with the estimated day of fledging or failure. The DSR estimates the probability that a given nest will survive on any given day during the breeding season, and is assumed to be constant throughout the nesting cycle. The overall nesting success rate for each bird species was calculated as DSR^x where x = total number of days of a complete nesting cycle based on estimates reported by Ehrlich et al. (1988). The overall nesting success rate estimates the probability that a given nest will survive an entire nesting cycle, from egg laying to fledging. The Mayfield method is preferred for estimating nesting success rates because it corrects for the potential bias associated with the greater likelihood of finding successful nests because they are active for longer periods than unsuccessful nests.

Nest site characteristics were measured at each nest following standard protocol (Martin et al. 1997). We measured nest height, nest substrate height, and nest substrate d.b.h. (diameter at breast height, 1.37 m above the ground). For ground-nesting birds, the nest substrate was defined as the closest plant stem within 30 cm of the nest; if no stems were within 30 cm, the nest was designated as "in open." The nest substrate d.b.h. was recorded as zero if the nest substrate was less than 1.37 m in height or if the substrate was rock. "Side cover" was estimated as the average percentage concealment of each nest at nest-height level from a height of 1 m from four cardinal directions (N, E, S, W). "Overhead cover" was estimated as the percentage concealment from 1 m above the nest.

Because the nest site variables were likely to be intercorrelated, we ran a principal components analysis (PCA) to reduce the dimensionality of the data set to a smaller set of uncorrelated variables that accounted for a large proportion of the variation in the original data set. Percentage variables were arcsine square-root transformed and other variables were square-root transformed prior to analysis to approximate a normal distribution (Zar 1984). The PCA was run on the transformed variables using the factor analysis procedure in SPSS (SPSS 9.0), and factor matrices were rotated with the varimax option. Differences in principal components scores among bird species and among nest fates (successful versus depredated and parasitized versus unparasitized) were assessed using one-way ANOVAs with post-hoc Tukey multiple comparisons (Zar 1984).

Results

Breeding Bird Densities

Densities of 29 breeding bird species were estimated based on the territory-mapping surveys (Table 1). The total population density per unit averaged 201.4 ± 9.0 pairs per 40 ha. Ovenbirds and red-eyed vireos were the most abundant species, with densities approaching 40 pairs per 40 ha (Table 1). Acadian flycatchers, scarlet tanagers, and wood thrushes were also common, with densities ranging from 12 to 26 pairs per 40 ha. Cerulean warblers, eastern wood-pewees, hooded warblers, and worm-eating warblers were less common, with densities of 6 to 9 pairs per 40 ha. Uncommon species included the indigo bunting, Kentucky warbler, and northern cardinal, each with densities of less than 1 pair per 40 ha.

Midstory-nesting birds were the most abundant of the nest site groups (Fig. 1a), represented primarily by the Acadian flycatcher, red-eyed vireo, and wood thrush. Ground-foraging birds were the most abundant of the foraging site groups (Fig. 1b), represented primarily by the ovenbird and wood thrush.

There were no significant differences in densities of individual bird species, densities of nest site groups or foraging site groups, or total densities among the three treatment units ($F_{2,9} < 5.7$, $p > 0.05$). Densities of several bird species varied by study area. The cerulean warbler was more common at AR and WR (12 and 15 pairs

Table 1.—Population densities (pairs per 40 ha), distributions of bird territories by integrated moisture index (IMI), and status of breeding bird species in mixed-oak forests, southern Ohio, 1995.

Species by nest site	Foraging site[a]	Mean Density (SE)	Proportion of territories by IMI[b] xeric	inter-mediate	mesic		Trends[c] Ohio	US	Area sensitive
Ground									
Black-and-white warbler (*Mniotilta varia*)	B	3.3 (0.8)	0.37	0.31	0.31		0	-	yes
Kentucky warbler (*Oporornis formosus*)	LS	0.4 (0.2)	0.24	0.07	0.69		0	-	yes
Louisiana waterthrush (*Seiurus motacilla*)	G	0.4 (0.3)	0	0	1.00	**	0	0	yes
Ovenbird (*Seiurus aurocapillus*)	G	38.9 (0.9)	0.34	0.39	0.27		0	+	yes
Wild turkey (*Meleagris gallopavo*)	G	+[e]	-	-	-		-	0	
Worm-eating warbler (*Helmitheros vermivorus*)	LS	8.0 (1.0)	0.16	0.35	0.27	***	0	0	yes
Low shrub									
Hooded warbler (*Wilsonia citrina)*	LS	7.2 (0.8)	0.40	0.44	0.17		0	0	
Indigo bunting (*Passerina cyanea*)	LS	0.1 (0.1)	0	0.50	0.50		-	-	
Midstory									
Acadian flycatcher (*Empidonax virescens*)	A	12.4 (1.4)	0.04	0.26	0.70	***	0	0	yes
American redstart (*Setophaga ruticilla*)	M	1.3 (0.7)	0.00	0.06	0.94	***	0	0	
American robin (*Turdus migratorius*)	G	0.0 (0.0)[f]	1.00	0	0		+	+	
Northern cardinal (*Cardinalis cardinalis*)	M	0.9 (0.4)	0.39	0.22	0.39		0	0	
Red-eyed vireo (*Vireo olivaceus*)	M	39.1 (2.0)	0.32	0.41	0.28		0	+	yes
Wood thrush (*Hylocichla mustelina*)	G	26.2 (2.0)	0.28	0.40	0.32		0	-	yes
Yellow-billed cuckoo (*Coccyzus americanus*)	M	2.4 (0.3)	0.26	0.50	0.24		-	-	yes
Canopy									
American crow (*Corvus brachyrhynchos*)	C	+	-	-	-		0	+	yes
Blue jay (*Cyanocitta cristata*)	C	+	-	-	-		+	-	
Blue-gray gnatcatcher (*Polioptila caerulea*)	C	3.6 (0.4)	0.39	0.35	0.26		0	0	yes
Cerulean warbler (*Dendroica cerulea*)	C	8.9 (2.2)	0.24	0.37	0.38		-	-	yes
Eastern wood-pewee (*Dendroica cerulea*)	A	6.0 (0.8)	0.50	0.31	0.19	*	-	-	yes

Table 1. cont.

Species by nest site	Foraging site[a]	Mean Density (SE)	Proportion of territories by IMI[b] xeric	inter-mediate	mesic		Trends[c] Ohio	US	Area sensitive
Ruby-throated hummingbird (*Archilochus colubris*)	C	+	-	-	-		+	+	
Scarlet tanager (*Piranga olivacea*)	C	12.2 (0.6)	0.31	0.38	0.31		0	0	yes
Summer tanager (*Piranga flava*)	C	0.5 (0.3)	0.76	0.24	0		0	0	yes
Yellow-throated vireo (*Vireo flavifrons*)	C	3.9 (0.6)	0.39	0.38	0.23		0	+	yes
Cavity									
Carolina chickadee (*Poecile carolinensis*)	C	1.4 (0.4)	0.24	0.44	0.32		0	-	
Downy woodpecker (*Picoides pubescens*)	B	1.8 (0.3)	0.34	0.36	0.30		0	-	
Great crested flycatcher (*Myiarchus crinitus*)	A	1.0 (0.4)	0.32	0.32	0.36		-	0	yes
Hairy woodpecker (*Picoides villosus*)	B	1.1 (0.3)	0.33	0.39	0.28		-	0	yes
Northern flicker (*Colaptes auratus*)	B	0.5 (0.3)	0.25	0.50	0.25		-	-	
Pileated woodpecker (*Dryocopus pileatus*)	B	+	-	-	-		0	+	yes
Red-bellied woodpecker (*Melanerpes erythrocephalus)*	B	4.4 (0.4)	0.34	0.47	0.19		0	+	yes
Tufted titmouse (*Baeolophus bicolor*)	C	5.9 (0.6)	0.27	0.39	0.34		0	+	yes
White-breasted nuthatch (*Sitta carolinensis*)	B	6.9 (0.7)	0.30	0.40	0.30		0	+	yes
Rock									
Eastern phoebe (*Sayornis phoebe*)	A	2.5 (0.7)	0.15	0.24	0.62	**	-	+	
Other									
Brown-headed cowbird (*Molothrus ater*)	G	+	-	-	-		-	-	

[a] Foraging sites: A = aerial; B = bole; C =canopy; G = ground; LS = low shrub; M = midstory.

[b] Chi-square tests used to compare observed and expected distributions of territories among IMI categories. Expected values calculated based on composition of four combined study areas: 31 percent xeric, 40 percent intermediate, 29 percent mesic. Asterisks represent significant differences between observed and expected values: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

[c] Population trends from Breeding Bird Surveys, 1966-1996 from Sauer *et al.* (1997). + = population significantly increased during time period ($p < 0.05$); - = population significantly declined during time period ($p < 0.05$); 0 = no significant change in population detected during time period.

[d] Area-sensitive = abundance of bird species increases as size of forest tract increases; designations from Robbins *et al.* (1989).

[e] + = bird species present in study area but densities not estimated because species was rarely observed (e.g. wild turkey), did not occur in well-defined territories (e.g. blue jay), or territory size was larger than treatment unit (e.g. pileated woodpecker).

[f] Baseline densities of American robins = 0.04 (0.03).

Table 2.—Relative abundance of forest bird species by geographic location. 0 = bird species not present; 1 = bird species comprised less than 1 percent of total breeding bird population; 2 = 1-4 percent of population; 3 = 5-9 percent of population; 4 = 10-19 percent of population. "Southern Ohio" includes data from Table 1 and data from other study areas (see footnote). Additional bird species are listed here but not in Table 1 to show differences in community composition by geographic location.

Bird species by nest site	Southeast U.S.	southern Ohio	northern Ohio	Northeast U.S.
Ground				
Black-and-white warbler	2	2	0	2
Kentucky warbler	1	2	1	1
Louisiana waterthrush	1	2	2	1
Ovenbird	3	3	4	4
Veery	0	0	1	2
Worm-eating warbler	2	2	0	2
Low shrub				
Hooded warbler	2	2	2	1
Indigo bunting	2	2	1	1
Rufous-sided towhee (*Pipilo erythrophthalmus*)	2	2	1	1
Midstory				
Acadian flycatcher	2	3	3	1
American redstart	1	1	4	3
American robin	1	1	1	1
northern cardinal	2	2	2	1
red-eyed vireo	4	4	4	4
wood thrush	3	3	3	2
Canopy				
Black-throated green warbler (*Dendroica virens*)	1	1	1	2
Blue-gray gnatcatcher	2	2	1	2
Cerulean warbler	1	3	3	0
Eastern wood-pewee	2	2	3	2
Pine warbler	4	1	0	0
Scarlet tanager	2	2	2	3
Summer tanager	2	2	0	0
Yellow-throated vireo	2	2	2	2
Cavity				
Black-capped chickadee	1	0	2	2
Carolina chickadee	3	2	0	0
Great crested flycatcher	2	2	2	2
Red-bellied woodpecker	1	2	1	0
Tufted titmouse	2	2	3	2
White-breasted nuthatch	2	2	2	2

References:

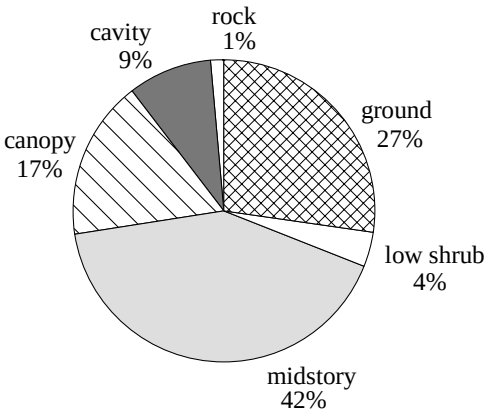
Southeast (Arkansas, Georgia, Tennessee, Virginia, West Virginia): Kendeigh 1944, Johnston and Odum 1956, Shugart and James 1973, Kendeigh and Fawver 1981, Cooper *et al.* 1990, Wilson *et al.* 1995, Salveter *et al.* 1996, Rodewald and Smith 1998.

Southern Ohio: this study, Breeding Bird Census database (surveys conducted in Adams, Hamilton, Hocking, Preble, and Scioto counties).

Northern Ohio: Williams 1936, Kendeigh 1944, Horn and Benninger-Truax 1997, Breeding Bird Census database (surveys conducted in Cuyahoga and Mahoning counties).

Northeast (Massachusetts, New York, Pennsylvania): Kendeigh 1944, Kendeigh 1946, Webb *et al.* 1977, Holmes *et al.* 1986, Rollfinke and Yahner 1990, DeGraaf *et al.* 1991, Yahner 1993.

a.) By nest site



b.) By foraging site

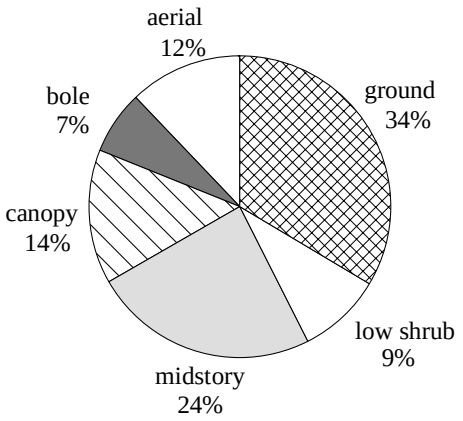


Figure 1.—Composition of breeding bird communities (percent of total density) in southern Ohio mixed-oak forests by nest site and foraging site.

respectively, per 40 ha), less common at YB (7 pairs per 40 ha), and uncommon at BR (1 pair per 40 ha). Eastern phoebes were more common at AR and YB (4 and 5 pairs respectively, per 40 ha) than at WR and BR (1 pair per 40 ha). The great crested flycatcher was observed more frequently at WR (4 pairs per 40 ha) than the other study areas (less than 1 pair per 40 ha).

Territories of six bird species were nonrandomly distributed with respect to IMI class (Table 1). The Louisiana waterthrush, worm-eating warbler, Acadian flycatcher, American redstart, and eastern phoebe occurred more frequently in mesic than xeric areas. The eastern wood-pewee occurred more frequently in xeric than mesic areas.

The breeding bird communities observed at our study areas were similar to those observed in eastern deciduous forests at other sites. Ovenbirds, red-eyed vireos, and wood thrushes were consistently the most abundant species, regardless of location (Table 2). Other common species present at most sites included the Acadian flycatcher, eastern wood-pewee, hooded warbler, scarlet tanager, and yellow-throated vireo. Cerulean warblers were observed most frequently in Ohio, in both mixed-oak and beech-maple forest types.

The DCA separated the sites primarily along a first axis which accounted for 61.3 percent of the summed eigenvalues of the ordination. The second axis accounted for an additional 28.0 percent of the summed eigenvalues. The bird communities in all but one oak-pine site were clearly separated, compositionally, from sites dominated by oak-hickory or beech-maple (Fig. 2a). By contrast, composition was similar among sites dominated by oak-hickory and beech-maple, as shown by the central overlap of sites in Fig. 2a. Also, DCA indicated that the composition of bird communities in southern Ohio differed from communities in northern Ohio (Fig. 2b). Bird communities in southern Ohio were more similar to communities in the Southeastern United States because of the presence of species with more southern distributions, including the Carolina chickadee and summer tanager (Table 2). Conversely, bird communities in northern Ohio were more similar to communities in the Northeastern United States because of the presence or higher abundance of species with more northern distributions, including the American redstart, black-capped chickadee, and veery.

Nesting Success

We monitored 239 active nests of 14 bird species, resulting in 2,768 observation days. Daily nest mortality due to predation accounted for the majority of nest failures for most species. Predation rates were highest for the ovenbird and wood thrush and lowest for the worm-eating warbler and Acadian flycatcher (Table 3).

Brown-headed cowbirds parasitized 23 nests. Nest failures due to parasitism occurred most frequently for the hooded warbler and worm-eating warbler (Table 3). These failures occurred either because the host parents abandoned the parasitized nest or because only cowbirds fledged from the nest. Parasitism rates varied among host species with highest rates observed for the hooded warbler and scarlet tanager, and intermediate rates for the worm-eating warbler, red-eyed vireo, and ovenbird. Only one Acadian flycatcher nest was parasitized and no eastern phoebe or wood thrush nests were parasitized.

Table 3.—Fate of active nests in 1995.

Bird species by nest site	Number of nests	Daily nest mortality rates by cause of failure			Daily survival rate (SE)	Overall survival rate	Cowbird parasitism rate[c]
		Predation	Other[a]	Parasitism[b]			
Ground							
Ovenbird	27	0.053	0.004	0	0.944 (0.01)	24.8	14.8
Worm-eating warbler	12	0.023	0	0.023	0.954 (0.02)	31.9	33.3
Low shrub							
Hooded warbler	9	0.032	0	0.021	0.947 (0.02)	28.4	66.7
Midstory							
Acadian flycatcher	52	0.027	0.001	0	0.972 (0.01)	44.5	1.9
Red-eyed vireo	19	0.047	0.047	0.005	0.949 (0.02)	26.8	15.8
Wood thrush	89	0.052	0	0	0.948 (0.01)	22.6	0
Other							
Eastern phoebe	15	0.030	0	0	0.970 (0.01)	33.4	0
Scarlet tanager	6	0.048	0.012	0	0.940 (0.03)	20.1	50.0
other[d]	10	-	-	-	-	-	20.0

[a] Other = nest failure due to abandonment (after eggs laid), adult mortality, or weather.
[b] Parasitism = nest failure due to brown-headed cowbird parasitism, either because host parents abandoned nest after parasitism or because only cowbirds fledged from nest and host's offspring did not survive.
[c] Cowbird parasitism rate = percentage of all nests parasitized by cowbirds, regardless of fate.
[d]Other = species with less than 5 monitored nests: American redstart (1 nest), eastern wood-pewee (1 nest), Kentucky warbler (1 nest), northern cardinal (2 nests), ruby-throated hummingbird (1 nest), yellow-billed cuckoo (4 nests).

Nest Site Selection

The principal components analysis produced two factors, PC1 and PC2, that accounted for 84 percent of the variation in the five original nest site variables (Table 4). PC1 was positively correlated with nest height, nest substrate height, and nest substrate d.b.h. PC2 was positively correlated with overhead cover and side cover.

PC1 and PC2 scores differed significantly among bird species (PC1: $F_{6, 165} = 102.3$, $p < 0.001$; PC2: $F_{6, 165} = 10.1$, $p < 0.001$). PC1 scores were arrayed along a continuum of nest heights and nest substrate sizes, from the ground-nesting ovenbirds and worm-eating warblers to the upper midstory-nesting Acadian flycatcher (Fig. 3). Acadian flycatchers consistently placed their nests higher off the ground, and in taller and larger diameter trees than other bird species, including the red-eyed vireo and wood thrush (Table 5). PC1 scores differed among species as follows: Acadian flycatcher > (red-eyed vireo = wood thrush) > hooded warbler > (ovenbird = worm-eating warbler) (Tukey $p < 0.05$). PC1 scores for eastern phoebe nests were intermediate, similar to PC1 scores for red-eyed vireo, wood thrush, and hooded warbler nests.

The eastern phoebe had higher PC2 scores than all other bird species except the ovenbird (Tukey $p < 0.05$; Figure 3). Overhead cover estimates were higher for the eastern phoebe than other bird species (Table 5); their nests, placed on cave-like rock faces, were concealed from above and from three of four sides by rounded rock walls. Side cover estimates were higher for the ovenbird, worm-eating warbler, and eastern phoebe than other bird species (Table 5).

PC scores did not differ between successful and depredated nests for the Acadian flycatcher, eastern phoebe, hooded warbler, ovenbird, red-eyed vireo, wood thrush, or worm-eating warbler (Table 6). PC1 scores were lower at parasitized than unparasitized nests for the hooded warbler, red-eyed vireo, and worm-eating warbler (Table 7), indicating that parasitized nests were placed at lower heights, in smaller diameter substrates, or in more open areas. PC2 scores were lower at parasitized than unparasitized nests for the red-eyed vireo, indicating that parasitized nests were less concealed by surrounding vegetation than unparasitized nests.

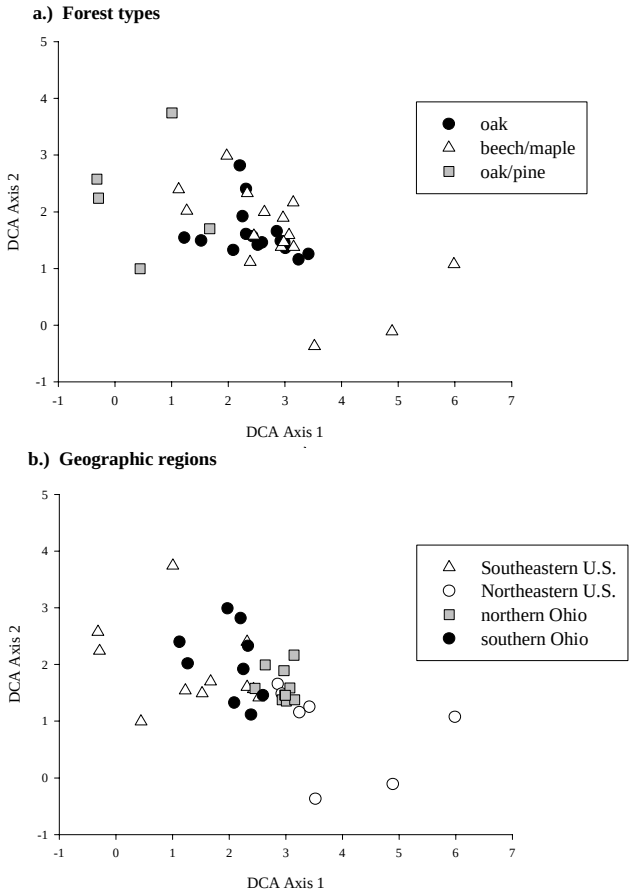


Figure 2.—Detrended correspondence analysis of breeding bird communities by forest type and geographic region.

Table 4.—results of principal components analysis nest site characteristics for the ovenbird, worm-eating warbler, hooded warbler, Acadian flycatcher, red-eyed vireo, wood thrush, and eastern phoebe.

	PC1	PC2
Total variance accounted for	56.4 %	27.4 %
Eigenvalue	2.823	1.374
Eigenvectors		
Nest height	0.937	-0.132
Nest substrate height	0.947	-0.041
Nest substrate DBH	0.884	-0.272
Overhead cover	-0.006	0.941
Side cover	-0.516	0.629

Discussion

Breeding Bird Community

Our surveys show that mixed-oak forests in southern Ohio provide habitat for at least 35 species of breeding birds. Species composition did not differ among the treatment units prior to the re-introduction of fire. Densities of three bird species, the cerulean warbler, eastern phoebe, and great crested flycatcher, varied among the four study areas. The cerulean warbler was more common at the Vinton County study areas (AR and WR) than the Lawrence County study areas (YB and BR). Cerulean warblers require mature forests of broadleaved deciduous trees, but they may occur in wet bottomlands, along mesic slopes, or upland ridges. Densities vary locally because individual territories are often clustered within suitable habitat; this clustering may facilitate social interactions between neighboring pairs, and is apparently unrelated to fine-scale variation in habitat conditions (Vanderah and Robinson 1995). By contrast, eastern phoebes require vertical rock faces for nesting, and densities of this species are likely to vary depending on the availability of these nest substrates. Great crested flycatchers nest in cavities. Densities of other cavity-nesting birds did not differ among the study areas, so availability of cavities probably was not a limiting factor; other factors potentially affecting population densities of the great crested flycatcher are unknown.

As described by Dettmers and Bart (1999), the abundance of some bird species varies across topographic gradients. Ovenbirds, red-eyed vireos, and wood thrushes were widely distributed throughout the treatment units, occurring on hillsides, ridgetops, and along streams. Eastern wood-pewees tended to occur primarily on dry hillsides and ridgetops. Acadian flycatchers, American redstarts, eastern phoebes, Louisiana waterthrushes, and worm-eating warblers were restricted primarily to stream bottoms and ravines.

Regional Status of Breeding Bird Species

Many of the species occurring at our study areas are declining in abundance nationwide. Twelve bird species, including 7 neotropical migrants, have experienced significant population declines in the United States during the last 30 years, as indicated by Breeding Bird Survey results (Sauer et al. 1997). Six of these twelve species (black-and-white warbler, blue jay, Carolina chickadee, downy woodpecker, Kentucky warbler, wood thrush) are declining in most of their range but are stable or increasing in Ohio. However, populations of the other six species (brown-headed cowbird, cerulean warbler, eastern wood-pewee, indigo bunting, northern flicker, and yellow-billed cuckoo) are declining both in Ohio and in other portions of their range in the United States.

Many bird species inhabiting our study areas are designated as area-sensitive, indicating a dependence on

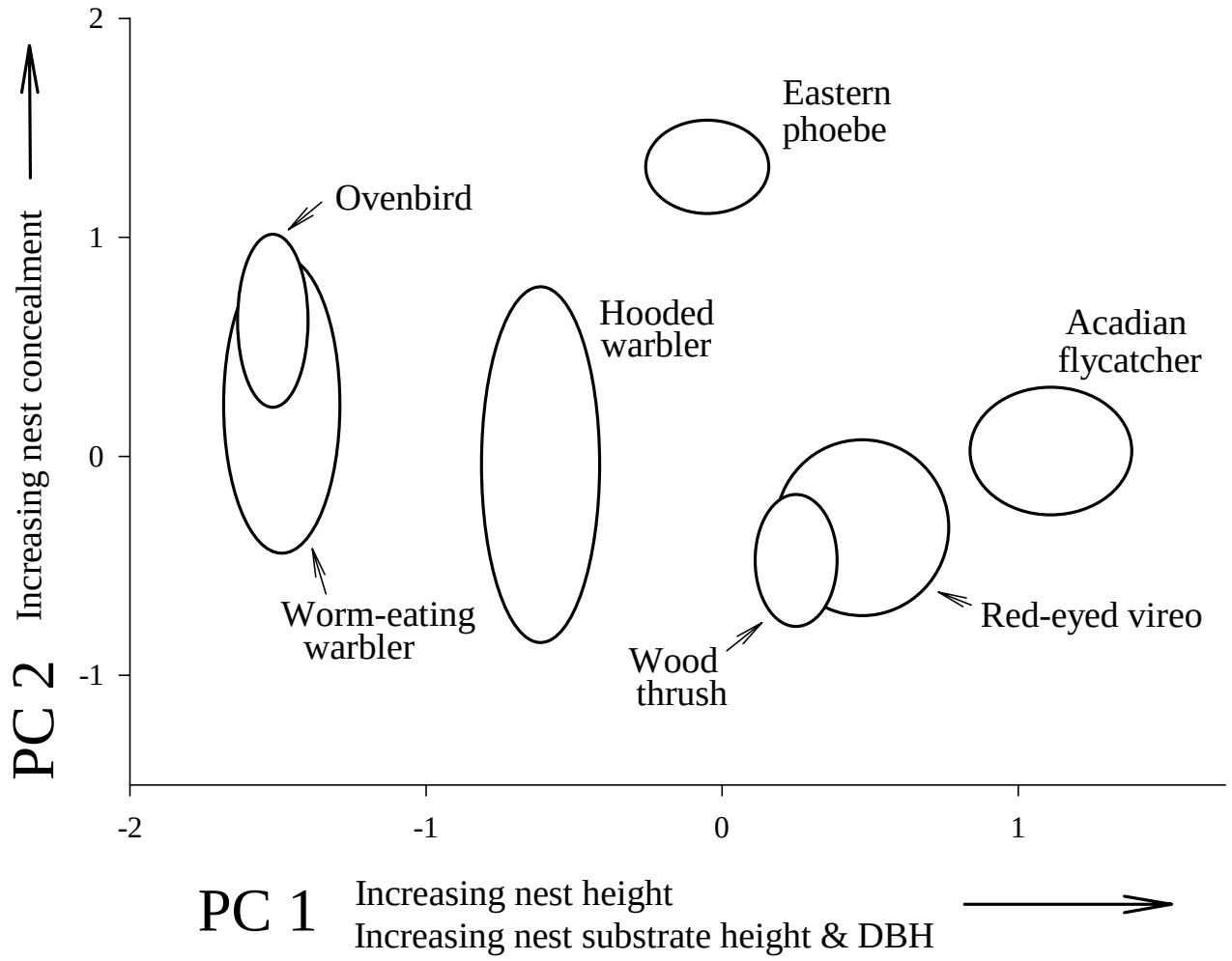


Figure 3.—Principal component analysis scores for nests in mixed-oak forests, southern Ohio.

large forest tracts and/or a sensitivity to forest fragmentation (Robbins et al. 1989). The extensive forest land in the Unglaciated Allegheny Plateau has been identified as an important area for providing large blocks of habitat that are likely to maintain populations of area-sensitive and declining species (Rosenberg and Wells 1995). Landscapes that are predominantly forested, such as those encompassing our study areas, appear to provide important habitat for three bird species in particular: the cerulean warbler, eastern wood-pewee, and wood thrush. These three species are common at our study areas, require mature forest habitat, and have shown population declines at both the regional and national level.

Importance of Oaks

Although forested landscapes are important for a number of bird species, the forest composition may be less critical. We found no difference in the species composition of breeding bird communities between mixed-oak and beech-maple forest types. Our analysis did not address differences in population levels because there was substantial variation in density estimates among the reported survey results. However, other studies have shown that bird population densities (for all species combined) were lower in mixed-oak forests than in mesic hardwood or beech-maple forests (Udvardy 1957, Probst 1979), although the reasons for these differences have not been investigated.

Mixed-oak forests are frequently identified as important wildlife habitat because acorns represent a valuable and energy-rich food resource, particularly during the non-breeding season (Healy et al. 1997). Our research focused specifically on the breeding bird community; only one-third of the species in this community are present during the non-breeding season and only two species (wild turkey and blue jay) regularly consume acorns. Bird species have developed a high degree of habitat selectivity, but the selectivity of birds inhabiting eastern deciduous forests may be based more on the structure of the vegetation, as illustrated by the different nest and foraging site requirements, than on the composition of the vegetation.

Table 5.—Mean nest site characteristics (SE) for the ovenbird, worm-eating warbler, hooded warbler, Acadian flycatcher, red-eyed vireo, wood thrush, and eastern phoebe.

Bird species by nest site	Nest height	Nest substrate height[a]	Nest substrate d.b.h.[b]	Side cover[c]	Overhead cover	Number of nests
Ground	—meters—		-cm-	—percent—		
Ovenbird	0 (0)	0.2 (0.04)	0 (0)	72 (5.2)	87 (4.6)	24
Worm-eating warbler	0 (0)	0.4 (0.09)	0 (0)	64 (4.2)	76 (9.4)	12
Low shrub						
Hooded warbler	0.6 (0.10)	1.4 (0.16)	0.4 (0.18)	21 (5.3)	78 (12.6)	9
Midstory						
Acadian flycatcher	3.8 (0.33)	10.0 (1.17)	7.7 (0.80)	22 (2.2)	70 (4.8)	35
Red-eyed vireo	2.6 (0.28)	5.3 (0.58)	4.1 (0.61)	19 (4.7)	64 (6.3)	17
Wood thrush	2.3 (0.11)	3.7 (0.27)	4.3 (0.28)	24 (2.3)	57 (4.7)	63
Rock						
Eastern phoebe	2.0 (0.24)	4.1 (0.47)	0 (0)	56 (4.3)	100 (0.0)	12

[a] Substrate for ground nests was the closest plant stem within 50 cm of the nest. If no stems were within 50 cm, the nest was designated as having no substrate.
[b] d.b.h. = 0 if substrate was less than 1.4 m in height or if substrate was rock.
[c] Side cover = mean of four values from each of four cardinal directions surrounding nest.

However, the presence of oaks does influence the composition of bird communities in other regions because oaks provide unique nesting or foraging substrates or because associated bird species are uniquely adapted to oaks. In northern Arizona, for example, pine-oak forests support more species of breeding birds than pine forests, in part because the low foliage of Gambel oaks (*Quercus gambelii*) provides more suitable cover for ground-nesting birds (Rosenstock 1998). In California, the acorn woodpecker (*Melanerpes formicivorus*) is one of the few bird species that is entirely dependent on oaks. Acorns are the primary food source of this species, but populations can be maintained only if multiple species of oaks are present to provide a reliable food supply (Bock and Bock 1974). Perhaps part of the reason more species of birds are not dependent on oaks is because acorn production tends to be irregular and unpredictable. Most species of oaks produce large acorn crops every 2 to 6 years, with low production or total failure in intervening years (Sork et al. 1993).

Other characteristics of oaks, such as the foliage and the associated arthropod community, are worth considering in terms of their value to breeding bird communities. Canopy-foraging birds may prefer some types of foliage over others because different arrangements of leaves may provide more accessible foraging surfaces or different types of hiding places for insects. For example, Holmes and Robinson (1981) found that canopy-foraging birds in New Hampshire preferred yellow birch (*Betula allegheniensis*) but avoided beech and sugar maple. These preferences were associated with higher densities and increased accessibility of insects on yellow birch foliage. Such comparisons have not been made among oaks, beech, and maple, though arthropod communities are likely to vary, particularly in response to differences in secondary compounds in the foliage. Oak foliage is high in tannin content, whereas red maple and yellow-poplar (*Liriodendron tulipifera*) foliage contains high concentrations of alkaloids. Gypsy moths (*Lymantria dispar*) consume tannin-laden oak leaves but avoid foliage containing alkaloids (Barbosa and Krischik 1987). Such preferences have not been identified for other species of foliage-consuming insects, though the implications of such preferences are substantial in terms of potential differences in food availability for canopy-foraging bird species.

Breeding Productivity

Assessing nesting success rates of different bird species is important in monitoring bird populations. Populations in an area may be high, but if breeding productivity and/or survival is not sufficient to sustain a local population, population stability will depend on immigration of dispersing individuals from surrounding areas. In the absence of immigration, such populations may become locally extinct (Van Horne 1983; Pulliam 1988). Monitoring breeding productivity thus provides an assessment of the health of local populations and provides

Table 6.—Mean principal component scores (SE) for successful and depredated nests.

Species		PC scores by nest fate: successful		PC scores by nest fate: depredated		*F*-value [a]	*N* [b]
Ovenbird	PC1	-1.46	(0.044)	-1.52	(0.044)	1.0	10, 13
	PC2	0.82	(0.164)	0.67	(0.182)	0.3	
Worm-eating warbler	PC1	-1.49	(0.114)	-1.55	(0.158)	0.1	8, 2
	PC2	0.18	(0.413)	0.21	(0.854)	0.0	
Hooded warbler	PC1	-0.71	(0.033)	-0.40	(0.183)	2.9	3, 3
	PC2	-0.08	(0.890)	-0.41	(0.556)	0.1	
Acadian flycatcher	PC1	0.99	(0.173)	1.14	(0.188)	0.4	16, 15
	PC2	-0.02	(0.161)	-0.03	(0.161)	0.0	
Red-eyed vireo	PC1	0.45	(0.262)	0.62	(0.156)	0.3	5, 9
	PC2	-0.44	(0.327)	-0.20	(0.263)	0.3	
Wood thrush	PC1	0.16	(0.129)	0.29	(0.057)	1.2	20, 39
	PC2	-0.61	(0.235)	-0.37	(0.164)	0.7	
Eastern phoebe	PC1	-0.07	(0.054)	-0.03	(0.177)	0.1	7, 5
	PC2	1.26	(0.084)	1.41	(0.125)	1.3	

[a] *F*-values from one-way ANOVAs testing for differences between successful and depredated nests.
[b] First number = number of successful nests; second number = number of depredated nests.

opportunities to identify different landscape or habitat features that directly influence reproduction (Martin 1992).

The primary factor affecting breeding productivity for many forest bird species is predation of nest contents (Martin 1992). Several studies have shown that nest predation rates for the wood thrush and other bird species were correlated with the extent of forest fragmentation (Donovan et al. 1995; Hoover et al. 1995; Robinson et al. 1995). As the extent of forest fragmentation increases, nesting success rates decline, apparently because nests become more accessible to predators associated with edge and open habitats surrounding smaller forest patches. Nesting success rates for wood thrushes at our study areas were lower than in other predominantly-forested landscapes (Donovan et al. 1995; Hoover et al. 1995; Robinson et al. 1995). Variation in nesting success rates may depend more on the local community of nest predators than on the extent of forest fragmentation (Yahner 1996). Eastern chipmunks (*Tamias striatus*) are common at our study areas and may be responsible for a high proportion of nest failures, but may be less common or absent in highly fragmented forests. Conversely, blue jays and American crows are among the primary nest predators in other regions and are present at our study areas, but are uncommon and do not appear to be responsible for a substantial proportion of wood thrush nest failures. Few studies have been conducted on variation in abundance, or differences in search behavior, diet, and activity patterns of potential nest predators. Future studies focusing on the behavior and abundance of nest predators may provide more precise identification of factors limiting productivity of wood thrushes and other bird species in different regions and landscape types.

A second factor affecting breeding productivity is parasitism by brown-headed cowbirds. For the wood thrush, cowbird parasitism rates vary regionally and with extent of forest fragmentation, with highest rates observed in highly fragmented landscapes in the Midwest, closer to the historic range of cowbirds (Hoover and Brittingham 1993; Donovan et al. 1995; Brawn and Robinson 1996). The absence of parasitism of wood thrush nests at our study areas was consistent with low rates observed in other predominately-forested landscapes (Donovan et al. 1995; Hoover et al. 1995). However, in our study areas, parasitism rates for nests of hooded warblers, ovenbirds, and worm-eating warblers were higher than in other studies, regardless of the extent of forest fragmentation (Hahn and Hatfield 1995; Winslow et al. 2000). Brown-headed cowbirds appear to be shifting their host preferences from the wood thrush to wood warblers as they expand their range eastward. Why is this apparent shift in host preference occurring? Perhaps cowbird nestlings are more successful in wood warbler nests than in wood thrush nests because they are more effective competitors against smaller nestmates. These cowbird nestlings then may become imprinted on their host

Table 7.—Mean principal component scores (SE) for unparasitized vs. parasitized nests. Results shown only for individual bird species with sample sizes of 2 or more parasitized nests.

Species		PC scores by nest fate				*F*-value [a]	*N* [b]
		successful		depredated			
Ovenbird	PC1	-1.51	(0.039)	-1.52	(0.033)	0.0	21, 3
	PC2	0.55	(0.187)	1.11	(0.129)	1.2	
Worm-eating warbler	PC1	-1.59	(0.092)	-1.27	(0.073)	5.1*	8, 4
	PC2	-0.06	(0.389)	0.83	(0.208)	2.4	
Hooded warbler	PC1	-0.41	(0.189)	-0.72	(0.027)	5.8*	3, 6
	PC2	0.40	(0.387)	-0.26	(0.458)	0.8	
Red-eyed vireo	PC1	0.61	(0.134)	-0.04	(0.159)	6.4*	13, 4
	PC2	-0.13	(0.184)	-0.95	(0.203)	5.4*	

[a] *F*-values from one-way ANOVAs testing for differences between unparasitized and parasitized nests. * = $p < 0.05$.
[b] First number = number of unparasitized nests; second number = number of parasitized nests.

parents and prefer to parasitize the same host species as adults, thus potentially leading to increased preferences for particular host species over multiple generations (Marchetti et al. 1998; Freeberg et al. 1999). Alternatively, cowbirds may be expanding their preferences as the rate at which they encounter more naive hosts increases in eastern regions (Lanyon 1992). Regardless of the explanation, cowbirds are likely to have a substantial impact on wood warblers if these high rates of parasitism are widespread. Fortunately, some potentially naive hosts are developing effective defenses against cowbirds. For example, hooded warblers have been sympatric with cowbirds for less than 200 years, and appear to be chosen preferentially as hosts. However, hooded warblers recognize cowbirds near their nests as threats (Mark and Stutchbury 1994) and frequently abandon parasitized nests, thus potentially reducing costs associated with high parasitism rates.

Population Sustainability

Are breeding productivity rates at our study areas high enough to sustain local populations? Populations are considered self-sustaining if daily nest survival rates are greater than 96 percent and brown-headed cowbird parasitism rates are less than 25 percent (Robinson 1996). Our results show that the eastern phoebe and Acadian flycatcher meet both these specifications, but other bird species listed in Table 3 do not, with daily nest survival rates less than 96 percent and/or cowbird parasitism rates over 25 percent. However, the upper portions of the 95 percent confidence intervals of the daily nest survival rates [DSR + (SE ´ 1.96)] for all bird species listed in Table 3 include 96 percent, suggesting that their populations may be self-sustaining in some situations.

An additional parameter that must be considered in assessing population health is seasonal fecundity, estimated as the number of fledglings produced per female per year. Daily nest survival rates were low for the wood thrush at our study areas, suggesting that productivity may be too low to sustain local populations. However, these low rates were offset by low cowbird parasitism rates and short renesting intervals. Wood thrushes renest soon after both failed and successful nesting attempts, with individual females nesting up to four times during a breeding season (Simons et al. 2000). Multiple nesting attempts increases the likelihood that any one attempt will be successful, thus enhancing a population's productivity and increasing the likelihood that populations are self-sustaining.

Acadian flycatchers, eastern phoebes, and hooded warblers also have multiple nesting attempts per year (usually two) even if the first attempt is successful (Walkinshaw 1966; Evans et al. 1994; Martin 1995), thus increasing the likelihood that populations are self-sustaining. This strategy is particularly beneficial for the hooded warbler because second nesting attempts are less likely to be parasitized by cowbirds than first nesting attempts (Artman and Dettmers, unpublished data). By contrast, the ovenbird and worm-eating warbler often have only one nesting attempt per year and may not renest if their first attempt is unsuccessful (Hann 1937; Hanners and Patton 1998). These two bird species thus may be more susceptible to reduced fecundity, potentially affecting the likelihood of populations being self-sustainable. Indeed, the daily nest survival rate for the ovenbird was one of the lowest of the species monitored. However, our sample sizes for ovenbirds and worm-eating warblers were relatively low, especially for the ovenbird,

considering it was one of the most abundant species at the study areas. These small sample sizes limit the precision of the daily survival rate estimates. In addition, monitoring these ground nests may have increased the likelihood of nest failure, thus biasing the daily nest survival estimates. To assess the extent of potential bias and obtain an additional measure of nesting productivity levels, future monitoring of ovenbirds and worm-eating warblers should include searches for fledglings in territories where nest contents are not directly monitored.

Nest Site Selection and Nesting Success

Though we found differences in nest site characteristics between parasitized and unparasitized nests for several bird species, we found no differences between successful and depredated nests. The conventional argument is that birds should respond to high rates of nest predation by selecting less vulnerable nest sites (Martin 1992). Selection of more concealed nest sites should reduce the search efficiency of predators and selection of higher nest sites should reduce accessibility of nests to predators (Martin 1993). However, support for these hypotheses has been variable. Concealment reduced the probability of nest predation for the hermit thrush (*Catharus guttatus*; Martin and Roper 1988) but not for the hooded warbler (Howlett and Stutchbury 1996; Kilgo et al. 1996), northern cardinal (Filliater et al. 1994), or wood thrush (Johnson 1997). Increasing nest height reduced the probability of nest predation for the Acadian flycatcher (Wilson and Cooper 1998) and American robin (Schmidt and Whelan 1999) but not for the wood thrush (Hoover and Brittingham 1998).

Why are these results so variable? In general, the effectiveness of strategies to avoid predation depends on the types of predators in the community and the search tactics they use to find prey (nests). Potential nest predators at our study areas include chipmunks, squirrels (*Sciurus* spp.), raccoons (*Procyon lotor*), black rat snakes (*Elaphe obsoleta*), and blue jays, each of which uses different types of foraging cues (visual, olfactory, auditory, chemosensory) and forages in different zones (ground, shrub, midcanopy). Increased nest concealment or increased nest height thus may reduce exposure to one type of predator while increasing exposure to another type of predator. In addition, the relative abundance or activity levels of different predators in the community may change as the nesting season progresses or from year to year (Schmidt 1997; McShea 2000), thus influencing the effectiveness of different strategies. Future monitoring should include identification of potential nest predators and assessment of their abundance and activity levels in the community. Such monitoring would increase our understanding of the factors potentially affecting breeding bird productivity.

Conclusions

The baseline data presented here will be used in assessing the effects of prescribed burning on the breeding bird community. The composition and abundance of breeding birds did not differ among the treatment units, prior to prescribed fire treatments. At a regional scale, populations of many bird species in the community are declining. These declines emphasize the need to continue to document trends in population levels and to assess potential changes in response to different management activities, including prescribed fire.

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Appendix

Publications (journal articles, theses/dissertations, reports) resulting from the research project described in this volume. Prescribed fires were conducted on the frequent burn units each year from 1996-1999 and on the infrequent burn units in 1996 and 1999. Nearly one-half of the citations listed below report post-fire results. Also included is research describing pre-burn conditions and research conducted on the study sites but not focusing on fire effects.

Artman, V. L. 2000. **Effects of prescribed burning on forest bird populations in southern Ohio.** Columbus, Ohio: Ohio State University. Dissertation. 172 p.

Artman, V. L.; Hutchinson, T. F.; Brawn, J. **Fire ecology and bird populations in eastern deciduous forests: a review.** Studies in Avian Biology. In press.

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Ohio in relation to prescribed fire and landscape position. Columbus, OH: Ohio State University. Dissertation. 102 p.

Dress, W. J.; Boerner, R. E. J. **Patterns of microarthropod abundance in oak-hickory ecosystems in relation to prescribed fire and landscape position.** Pedobiologia. In press.

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Sutherland, Elaine K.; Hutchinson, Todd F., eds. 2003. **Characteristics of mixed-oak forest ecosystems in southern Ohio prior to the reintroduction of fire**. Gen. Tech. Rep. NE-299. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 159 p.

Contains 12 chapters describing baseline conditions of mixed-oak forest ecosystems in the context of a long-term study of prescribed fire effects.

Keywords: ecosystem management, restoration, oak, prescribed burning, forest history, topographic gradients, moisture index, soil nutrients, understory vegetation, overstory, tree regeneration, light, foliar nutrients, birds, arthropods, diversity

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