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-m^2 subplots for each plot).

		IMI class			Study area			
Size class	Total (N = 108)	Xeric (N = 40)	Intermediate (N = 32)	Mesic (N = 36)	WR (N = 27)	AR (N = 27)	YB (N = 27)	BR (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.

			IMI Class			Study Area			
Species	Sz	Total N=108	Xer N=40	Int N=32	Mes N=36	WR N=27	AR N=27	YB N=27	BR 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	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					
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).

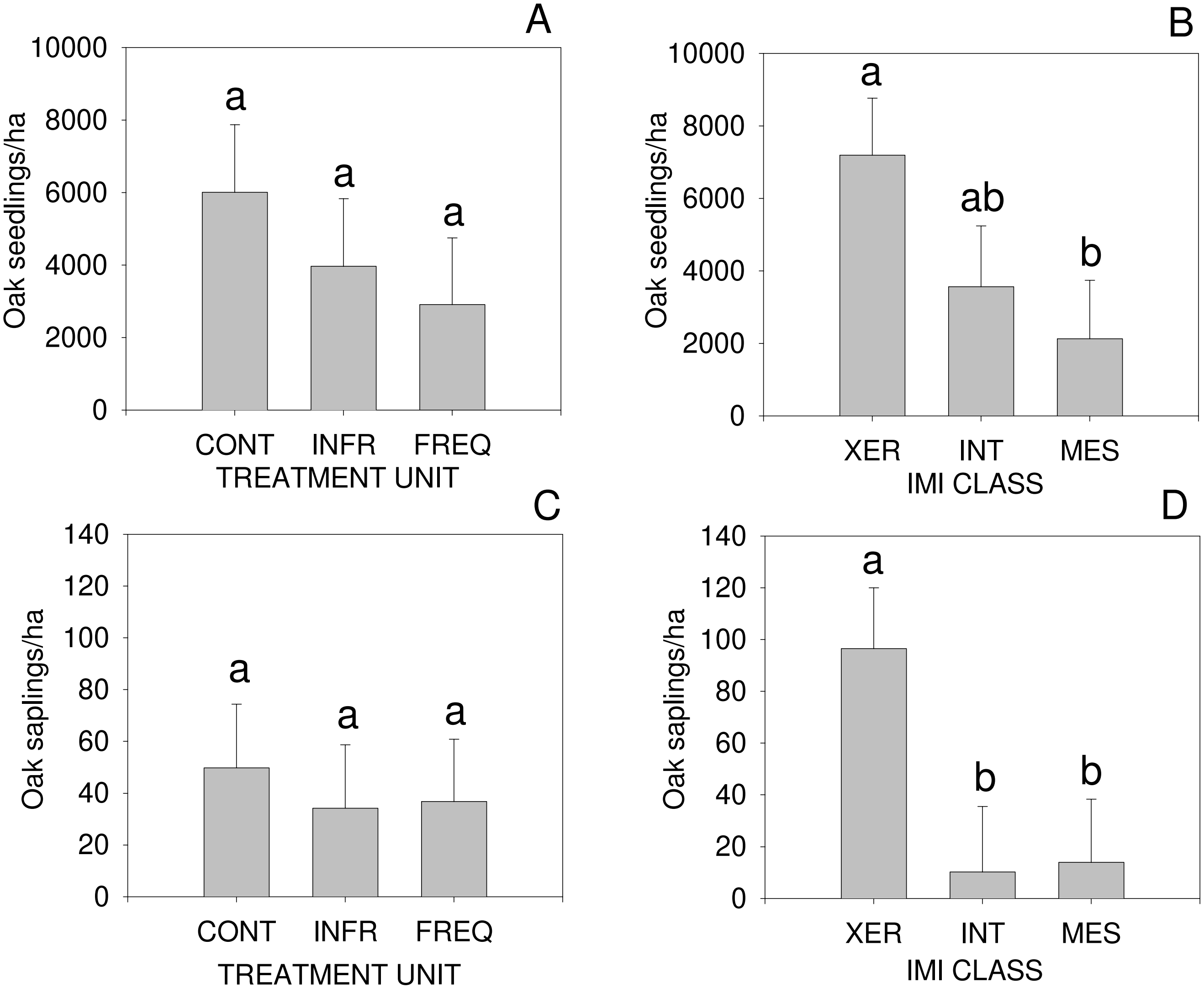

Figure 1. -- A. Oak seedling densities among the treatment units (CONT = control; INFR = infrequent; FREQ = frequent), prior to treatment; B. Oak seedling densities among the three IMI (moisture) classes (XER = xeric; INT = intermediate; MES = mesic); C. Oak sapling densities among the treatment units; 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).

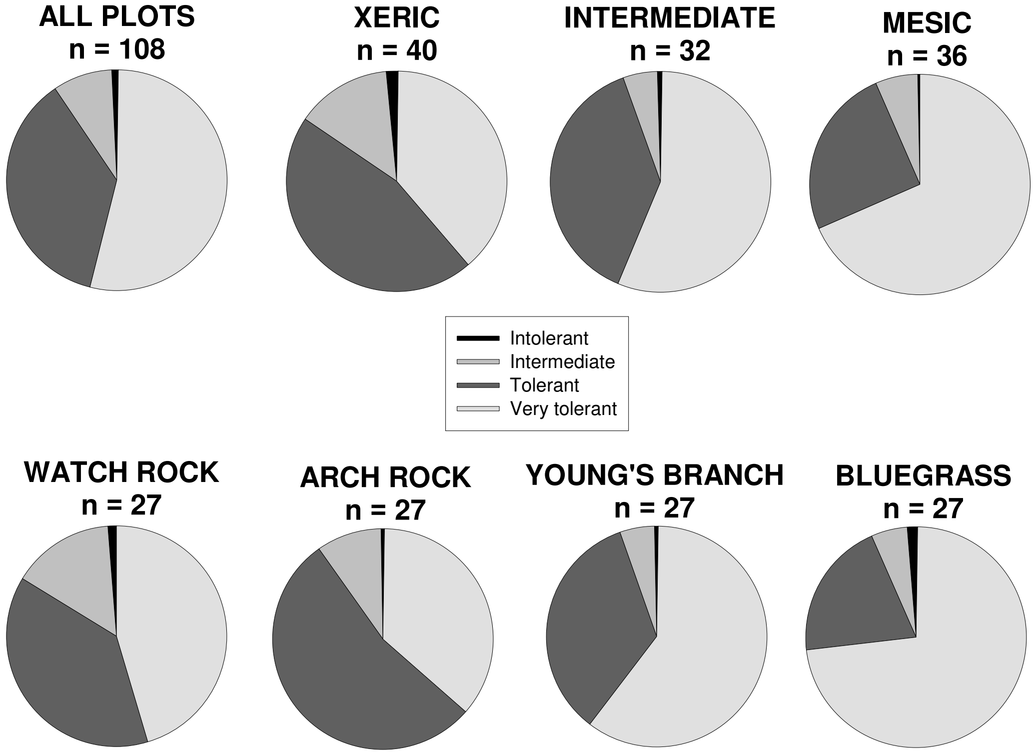

Figure 2.-- Relative density of sapling groups based on shade tolerance classifications. All sapling size classes were combined and species that cannot attain overstory stature (e.g. dogwood) are included. Shade tolerance classifications were from Burns and Honkala (1990), Iverson et al. (1999), and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

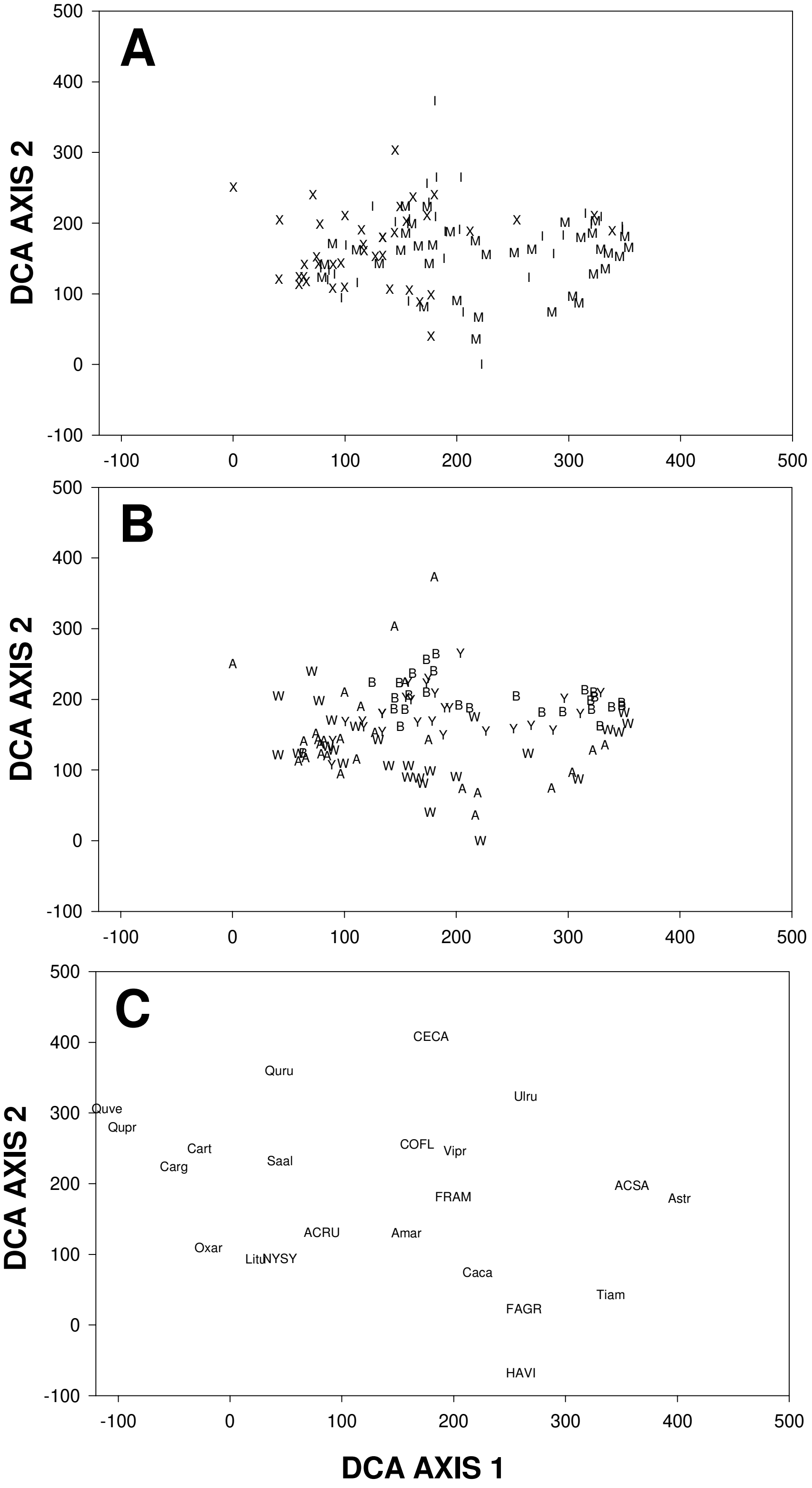

Figure 3.--Detrended correspondence analysis of the sapling subplots. A. Ordination of the 108 plots classified by IMI: X = xeric, I = intermediate, and M = mesic. B. Ordination of the 108 plots classified by study area: A= Arch Rock, W = Watch Rock, Y = Young's Branch, and B = Bluegrass Ridge. C. Ordination 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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