OAK FOREST COMPOSITION, SITE QUALITY, AND DYNAMICS IN RELATION TO SITE FACTORS IN THE SOUTHEASTERN MISSOURI OZARKS

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Abstract—Physical site factors are known to affect forest species composition but the pattern and variation across forest landscapes has not been well quantified. We discuss relationships between site factors including soil parent materials, depth to dolomite bedrock, aspect, and landform position and the distribution of vegetation, site index, and short-term succession in oak forests in the southeastern Missouri Ozarks. Overall, we found few strong relationships between these site factors and tree species composition except black oak (*Quercus velutina* Lam.) was more abundant on summit and shoulder landform positions. On average, site index was three to five ft. greater on backslopes than on summits and four ft. greater on north-facing slopes than on south-facing slopes. In the absence of disturbance, white oak (*Q. alba* L.) was generally succeeding species in the red oak group, especially on upper landforms.

INTRODUCTION

In most parts of the Central Hardwood Region, physical site factors are important determinants of species composition, site quality, and successional trends (e.g., Johnson and others 2002, Nigh and others 2000, VanKley and others 1994). Although general trends in species composition related to aspect, landforms, and soil conditions are readily recognized by experienced resource managers, the magnitude of those differences and the variation in responses across similar sites has not been well quantified.

The Missouri Ozark Forest Ecosystem Project (MOFEP) is an on-going, centuries-long experiment that is evaluating the effects of even-aged, uneven-aged, and no-harvest management on a wide array of forest attributes, including overstory and understory vegetation, wildlife populations, mast production, insects, and fungi (Brookshire and Shifley 1997, Shifley and Brookshire 2000, Shifley and Kabrick 2002). An initial part of that experiment was the detailed mapping of soils and landforms and the detailed inventory of forest overstory and understory vegetation (Grabner 2000, Jensen 2000, Kabrick and others 2000, Shifley and others 2000). This has afforded a unique opportunity to examine the relationship of site factors to species composition across nearly 9,400 acres of mature, relatively undisturbed, second-growth Ozark forest.

Grabner (2002) found that depth to dolomite, geology and soil order (which together reflect major physical and chemical differences of soil parent materials in the study region), slope aspect, and landform position were important site factors for identifying and distinguishing different ecological landtypes and landtype phases in the MOFEP study region. These site factors affect the availability of light energy, nutrients, and water. In this paper, we evaluate the relative importance of each of these site factors for explaining differences in oak species composition and growth relative to other tree species and to forest site quality in Missouri

Ozark forests. Specific objectives were to (1) quantify the composition and growth of oaks and other overstory species in relation to the site factors of landform, aspect, depth to dolomite bedrock, and parent materials, and (2) relate those site factors to site index which has traditionally been used to evaluate site quality in the region.

METHODS MOFEP Site Description

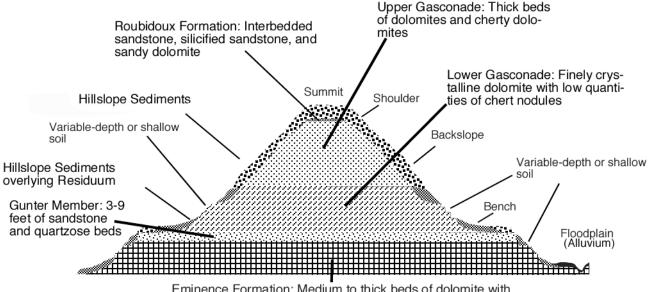
The MOFEP study and experimental design is described elsewhere in detail (Brookshire and Hauser 1993, Brookshire and Shifley 1997, Kurzejeski and others 1993, Sheriff 2002, Shifley and Brookshire 2000). The study consists of nine sites ranging in size from 657 ac to 1,302 ac, primarily within the Current River Oak Forest Breaks and the Current River Oak-Pine Woodland Hills landtype associations of the Ozark Highlands. The Current River Oak Forest Breaks has narrow ridges and steep sideslopes with relief of 300-450 ft, which exposes the Roubidoux. Gasconade, and Eminence formations. The Current River Oak-Pine Hills has broad ridges with relief <300 ft and exposes only the Roubidoux and Gasconade bedrock formations. Upland soils of these landtype associations are primarily Ultisols and Alfisols formed in highly weathered hillslope sediments or residuum; soils in upland waterways and bottomlands are primarily Ultisols and Alfisols formed in gravelly alluvium (Kabrick and others 2000; Meinert and others 1997).

Vegetation Sampling and Site Index Determinations

There are 648 permanent vegetation plots distributed roughly equally among the nine MOFEP sites. Since 1991, these permanent plots have been re-inventoried approximately every three years to document the condition of woody vegetation. Within permanent plots, live and dead trees ≥ 4.5 in. diameter at breast height (d.b.h.) are

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Eminence Formation: Medium to thick beds of dolomite with small amounts of chert

Landform	Description		
Backslope	The landscape position that forms the steepest inclined surface and principle element of many hillslopes. Slopes > 20%. Contains sideslope, noseslope and headslope components.		
Bench	A narrow, nearly level to slightly sloping platform breaking the slope continuity. Typically occurs on backslope positions in the Ozarks where underlying bedrock is more resistant to weathering than layers above or below. Slopes 0-20%.		
Flood Plain	The nearly level plain that borders a stream and is subject to inundation under floodstage conditions. Slopes 0-4%.		
Shoulder	The landscape position that forms the upper most inclined surface near the top of a hillslope. It is commonly convex in shape and comprises the transition from summit to backslope. Slopes 8-20%. Also includes shoulder ridges which are narrow, convex ridgetops.		
Summit	The topographically highest hillslope position of a hillslope profile and exhibiting a nearly level surface. Slopes 0-8%.		

Figure 1—Illustration of hill cross section showing typical locations of bedrock geology, landforms, soil parent material, and soil depth to bedrock. Definitions for landforms are included. See Methods for definitions of soil parent material, soil depth to bedrock, and aspect classes.

sampled in 0.5-ac circular plots; trees between 1.5 and 4.5 in. d.b.h. are sampled in four 0.05-ac circular subplots; trees at least 3.3 ft tall and less than 1.5 in. d.b.h. are sampled in four 0.01-ac circular subplots nested within the 0.05-ac subplots. Characteristics recorded for each tree include species, d.b.h. or size class for trees < 1.5 in. d.b.h., and status (e.g., live, dead, den, cut, blow-down). Plot and subplot data were combined to obtain plot averages by d.b.h. or size class and all values are converted to an acre basis for analysis.

From 1993 to 1996, site index was determined on suitable trees at MOFEP. Trees considered suitable were canopy codominants having good form with no indication that they had been suppressed and showing the best growth potential. One to five candidate trees selected for site index determination were sampled outside of the 0.5 ac permanent vegetation plots but within 330 ft of vegetation plots. Tree distance and azimuth from the geo-referenced vegetation plot center were recorded for each site index tree and later used to determine the latitude and longitude of each site

index tree. Trees were assigned a ranking of their perceived quality for indicating site index. Tree heights were measured with clinometer to the nearest ft. A single increment core was extracted at breast height and taken to the lab for age determination. Site index was determined using species, height, age at d.b.h., and published site index equations for species in the Missouri Ozarks (McQuilkin 1974, 1978; Nash 1963).

Soil and Site Characterization

A detailed landscape-scale soil mapping project was conducted on MOFEP in 1994-1995 (Kabrick and others 2000; Meinert and others 1997). This included characterizing geomorphology, geology, and soil characteristics of each permanent MOFEP vegetation plot. Laboratory data generated from 120 soil excavations was correlated to the soil-landscape map units. Detailed information about the soil-landscape mapping and soil characterization data can be found in Kabrick and others (2000), Meinert and others (1997), and data available through the Missouri Department of Conservation.

Site Factors and Variables Used in this Study

We considered four site factors: landform position, parent material, aspect, and depth to bedrock. Definitions of landforms follow those used for routine soil surveys and are defined in figure 1. Soil parent materials were alluvium, hillslope sediments (Daniels and Hammer 1992), and hillslope sediments overlying residuum. At MOFEP, alluvium contained 35 to 60 percent cherty gravel and/or cobbles, clays having mixed mineralogy, cation exchange capacities (CEC) of 2-22 cmol(+)kg-1, and base saturations (BS) of 2-60 percent. Hillslope sediments generally had 15-60 percent cherty gravel, kaolinitic mineralogy, CEC <20 cmol(+)kg-1, and BS of 5-55 percent. Residuum, primarily from dolomite, had < 15 percent gravel, mixed or smectitic mineralogy, CEC 5-40 cmol(+)kg⁻¹, and BS of 30-100 percent. Aspect classes were protected (316-135 degrees), and exposed (136-315 degrees). Site depths to bedrock were classified as deep (>48 in. throughout), variable depth (10-50 percent dolomite out crop; soil depth 0 to >48 in.), or shallow (glades with >50 percent dolomite outcrop and soil depth <48 in.).

To evaluate relationships between species composition and site factors, we selected a subset of 310 MOFEP vegetation plots that were each uniform with respect to site factors. Because harvest treatments on MOFEP that began in 1996 reduced the number of undisturbed plots available, we used data inventoried in 1994-1995, prior to implementing harvest treatments, for our analysis. Response variables included mean number of trees per acre and mean basal area per acre for white oak, post oak, scarlet oak, black oak, and for other oaks and tree species combined.

To evaluate site quality relationships, we used site index estimates made from 289 white oaks and 706 black oaks. These two species were selected because they were most abundant site index tree species at MOFEP. Because site index trees were located outside of the permanent vegetation plot boundaries, we identified site factors of each site index tree by projecting the geo-referenced tree locations

onto the soil-landscape map with GIS software. We then estimated individual site factors associated with each site index tree using the soil-landscape information database.

To evaluate dynamics, we selected a subset of 210 MOFEP vegetation plots that were each uniform in site factors and had not been harvested or thinned during the period from the first MOFEP inventory in 1991-1992 and the most recent inventory completed in 2001-2002. We then calculated the mean change in basal area of trees ≥ 4.5 in. d.b.h. from the first to the most recent inventory. This was done for white oak, post oak, scarlet oak, black oak, other oaks (combined), and all other tree species (combined).

RESULTS

Oaks are the dominant trees at MOFEP (table 1). The four most abundant oaks, black oak, scarlet oak, white oak, and post oak, together comprise nearly 71 percent of the total basal area. Chinkapin oak, blackjack oak, Shumard oak, and northern red oak also occur, but together they comprise 1 percent of the basal area. Shortleaf pine, pignut hickory, black hickory, mockernut hickory, blackgum, and flowering dogwood are also abundant and important species of Missouri Ozarks forests and woodlands.

We found few strong relationships between selected site factors and tree species composition. Black oak basal area was relatively greater on upper landforms than on lower landforms, and both black oak and scarlet oak basal area were greater on soils formed in hillslope sediments than on soils formed in other parent materials (fig. 2). White oak and post oak basal areas were slightly greater on benches than on other landforms. Post oak basal area was slightly greater on soils formed in alluvium than on soils in other parent materials and on soils variable in depth to dolomite than on deep soils or shallow soils. The basal area of "other oaks," of which chinkapin oak was most abundant, was greatest on shallow soils.

White oak site index was approximately three ft. less than black oak site index regardless of site factor (fig. 3), illustrating the well-documented height growth rate difference between these two species (Carmean and others 1989). White oak and black oak site index each were greater on backslopes and less on summits. We also found the site index for each species to be four feet greater on protected (316-135 degrees) aspects than on exposed (136-315 degrees) aspects. Site index was considerably lower on shallow soils than on soils that were deep or variable in depth to dolomite.

During the past decade, white oak basal area increased considerably regardless of the site factors and increased the most on benches (fig. 4). Post oak basal area also increased, and relatively large net growth increases occurred on both upper and lower landforms, in alluvium, and in soils that were either variable in depth or shallow to dolomite bedrock. Most notably, both scarlet oak and black oak basal area decreased on summits and shoulders and black oak basal area also decreased on benches. The category "other oaks," which is mostly composed of chinkapin oak, increased primarily on sites having soils that were variable in depth or shallow to dolomite bedrock. The basal areas of "other

Table 1—The 48 tree species observed on 648 MOFEP vegetation plots

Scientific name	Common name	Basal area	Trees per acre
		ft²/ac	no.
Quercus velutina Lam.	Black oak	23.2	58
Q. coccinea Muenchh.	Scarlet oak	20.3	49
Quercus alba L.	White oak	19.6	130
Pinus echinata Mill.	Shortleaf pine	8.0	21
Quercus stellata Wangenh.	Post oak	5.8	22
Carya glabra (Mill.) Sweet	Pignut hickory	3.8	49
C. texana Buckl.	Black hickory	3.6	44
C. tomentosa Poir. Nutt.	Mockernut hickory	3.4	56
Cornus florida L.	Flowering dogwood	3.2	349
Nyssa sylvatica Marsh.	Blackgum	2.3	86
Quercus muehlenbergii Engelm.	Chinkapin oak	0.6	5
Q. marilandica Muenchh.	Blackjack oak	0.5	3
Acer rubrum L.	Red maple	0.4	54
Sassafras albidum (Nutt.) Nees	Sassafras	0.4	104
Juglans nigra L.	Black walnut	0.3	1
Ulmus rubra Muhl.	Slippery elm	0.3	20
U. alata Michx.	Winged elm	0.3	19
Fraxinus americana L.	White ash	0.2	18
Juniperus virginiana L.	Red cedar	0.1	3
Acer saccharum Marsh.	Sugar maple	0.1	3
Quercus shumardii Buckl.	Shumard oak	0.1	1
Q. rubra L.	Northern red oak	0.1	< 1
Carya cordiformis (Wangenh.) K. Koch	Bitternut hickory	0.1	1
Ulmus americana L.	American elm	0.1	4
Rhamnus caroliniana Walt.	Carolina buckthorn	0.1	36
Cercis canadensis L.	Redbud	0.1	16
Morus rubra L.	Red mulberry	< 0.01	4
Diospyros virginiana L.	Persimmon	< 0.01	6
Amelanchier arborea (Michx. f.) Fern.	Serviceberry	< 0.01	7
Crataegus spp.	Hawthorn	< 0.01	4
Prunus serotina Ehrh.	Black cherry	< 0.01	5
Bumelia lanuginosa (Michx.) Pers.	Gum bumelia	< 0.01	3
Carya ovata (Mill.) K. Koch	Shagbark hickory	< 0.01	< 1
Celtis occidentalis L.	Hackberry	< 0.01	9
Viburnum rufidulum Raf.	Rusty black haw	< 0.01	7
Fraxinus pennsylvanica Marsh.	Green ash	< 0.01	2
Carpinus caroliniana Walt.	Hornbeam	< 0.01	3
Gleditsia triacanthos L.	Honey locust	< 0.01	< 1
Prunus americana Ehrh.	Wild plum	< 0.01	1
Ostrya virginiana (Mill.) K. Koch	Ironwood	< 0.01	< 1
Asimina triloba (L.) Dunal	Pawpaw	< 0.01	8
Rhus copallina L.	Winged sumac	< 0.01	1
Celtis laevigata Willd.	Sugarberry	< 0.01	1
C. tenuifolia Nutt.	Dwark hackberry	< 0.01	2
Rhus glabra L.	Smooth sumac	< 0.01	1
Elaeagnus umbellata Thunb.	Autumn olive	< 0.01	< 1
Robinia pseudoacacia L.	Black locust	< 0.01	< 1
Staphylea trifolia L.	Bladdernut	< 0.01	< 1

species," mostly comprised of shortleaf pine, and the three most common hickories, increased regardless of site factors.

DISCUSSION

Oaks are the most dominant genera of trees in our study area and comprise most of the basal area regardless of

landform, soil parent materials, aspect classes, and depths to and extent of dolomite bedrock. This differs from mesophytic forests of the Central Hardwood Region found north and east of the Missouri Ozarks where oaks are components of more diverse forests and where oaks are often restricted to drier sites such as on ridge tops and south-facing slopes (Johnson and others 2002). This suggests that the condi-

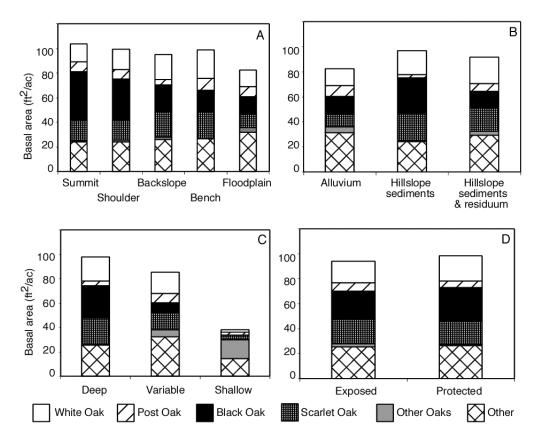


Figure 2—Proportion of mean basal area by species group and (A) landform, (B) soil parent material, (C) soil depth to bedrock, and (D) aspect.

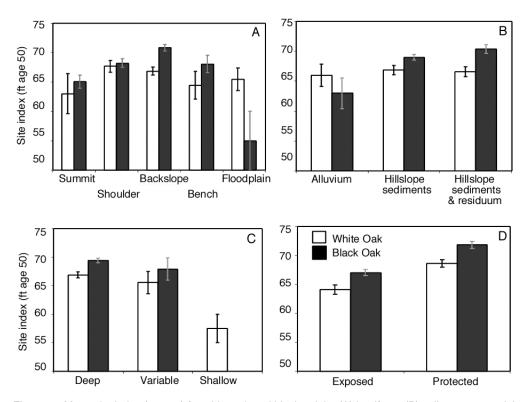


Figure 3—Mean site index (age 50) for white oak and black oak by (A) landform, (B) soil parent material, (C) soil depth to bedrock, and (D) aspect. There were no black oak site index trees on shallow soils, panel (C).

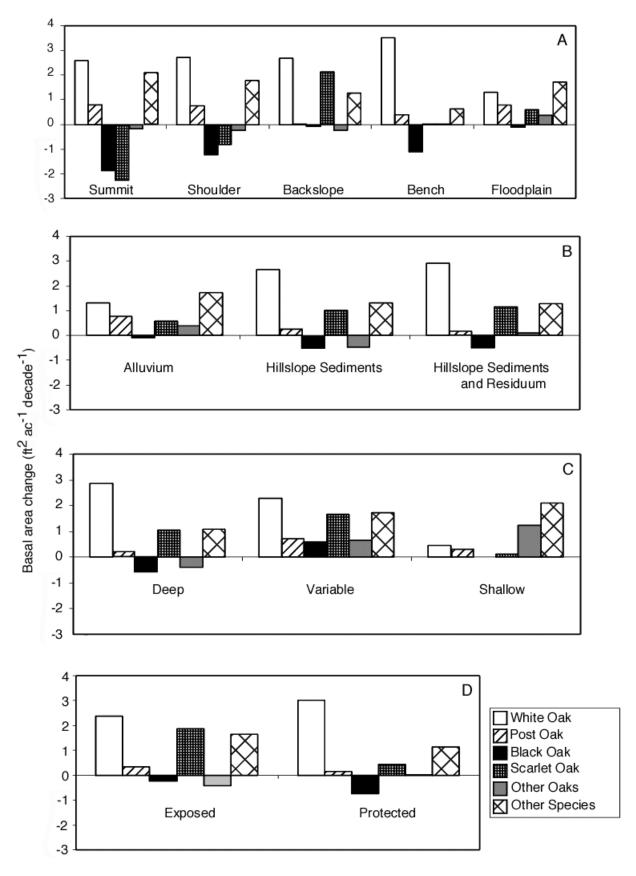


Figure 4—Mean net basal area growth (ft^2 ac⁻¹ decade⁻¹) by species group and (A) landform, (B) soil parent material, (C) soil depth to bedrock, and (D) aspect for trees ≥ 4.5 in. diameter at breast height.

tions of our study area are generally drier, and therefore they restrict development of many of the mesic species that are abundant elsewhere in the Central Hardwoods Region. Moreover, oaks are adapted to fire (Guyette and Dey, 1997; Johnson and others 2001), an important disturbance throughout the Ozarks for hundreds of years prior to extensive fire suppression efforts beginning around 1940 (Batek and others 1999, Guyette and Dey 1997). Most evidence suggests that fire in the pre-European landscape also maintained a more open woodland structure in our study region rather than the closed-canopy forests present today (Batek and others 1999).

In our analysis, the species composition differences related to site factors were subtle. The most prominent relationships were that black oaks were more abundant on drier landforms such as summits and shoulders than on other landforms and both black oaks and scarlet oaks were more abundant in soil parent materials having a low water holding capacity and low nutrient supply than in other soil parent materials. Evidence from remnant stumps indicates that in the pre-European landscape, shortleaf pines were once much more prominent on these drier and nutrient-poor sites than they are today (Guyette and Dey 1997). Guyette and Dey (1997) attribute relatively low abundance of shortleaf pine in these sites today to the extensive pine harvesting during the late 1800's and early 1900's followed by frequent burning. It appears that black oaks, and to some degree scarlet oaks are now most abundant in sites that historically supported more shortleaf pines.

Both black oaks and scarlet oaks are susceptible to decline as they mature, particularly on droughty, nutrient-poor sites (Johnson and others 2002). At MOFEP, most of the black oak and scarlet oak basal area is from older, large-diameter trees. Our data show that black oaks on all sites had a net growth loss due to high mortality and both black oak and scarlet oak net growth losses were particularly great on summits and shoulders. On undisturbed sites, white oaks appear to be replacing black oaks and scarlet oaks and are increasing in basal area regardless of the site factors. Compared to black oaks and scarlet oaks, white oaks are more shade tolerant, live longer, and are less susceptible to oak decline. Consequently, white oaks had a greater ingrowth rate and lower mortality rate than either black oaks or scarlet oaks. Post oaks are also increasing in dominance, but at a much slower rate because of their slow growth rate and because their shade intolerance limits their regeneration in the absence of disturbances. Much like white oaks, post oaks are long lived and not considered very susceptible to decline. Relatively large net growth increases by post oaks occurred where post oaks were particularly abundant such as on both upper and lower landform positions, in alluvium, and in variable depth and shallow soils. Of the common, "other species," shortleaf pine, pignut hickory, black hickory, and mockernut hickory had the greatest net basal area increases, largely due to moderate growth rates of residual trees and low mortality rates during the sampling period (data not shown).

Site quality, as determined by site index, was more closely related to site factors than was species composition. Landform position and aspect were the two most important factors followed by depth to or extent of dolomite bedrock and soil parent materials. Specifically, our data suggest that the highest site indices for both white oaks and black oaks occurred on protected backslopes where soils were deep and were formed in hillslope sediments overlying residuum. These particular site factors thus indicate where water and nutrients are more available and where rooting volume is greater.

It is important to recognize that the four site factors evaluated in our study are not completely independent of one another. For example, soils that are shallow to bedrock occur more frequently on exposed aspects, and alluvium is found nearly exclusively in floodplains. Clearly, these site factors must be used in combination as is the practice in ecological classification schemes such as the one that Grabner (2002) developed for the MOFEP study area. Our analysis quantified relationships among the composition, site quality, and growth of oaks and other trees species, and site factors most important for identifying and distinguishing ecological land types and phases in the southeastern Missouri Ozarks.

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