Photo by Jeffrey Lee

Community Range

- ■ Prevalent or likely prevalent
- ■ Infrequent or likely infrequent
- □ Absent or likely absent

Overview: Dry-mesic southern forests are oak-dominated forests occurring south of the climatic tension zone in Michigan's Lower Peninsula on coarse-textured moraines, ice-contact terrain, sandy outwash plains, sandy lake plains, and sand dunes. They are typified by well-drained to somewhat excessively drained soil and were characterized by episodic fires prior to European settlement. Historically, these communities typically occurred over a broad landscape matrix interspersed with prairies, oak savannas, mesic forests, and wetlands.

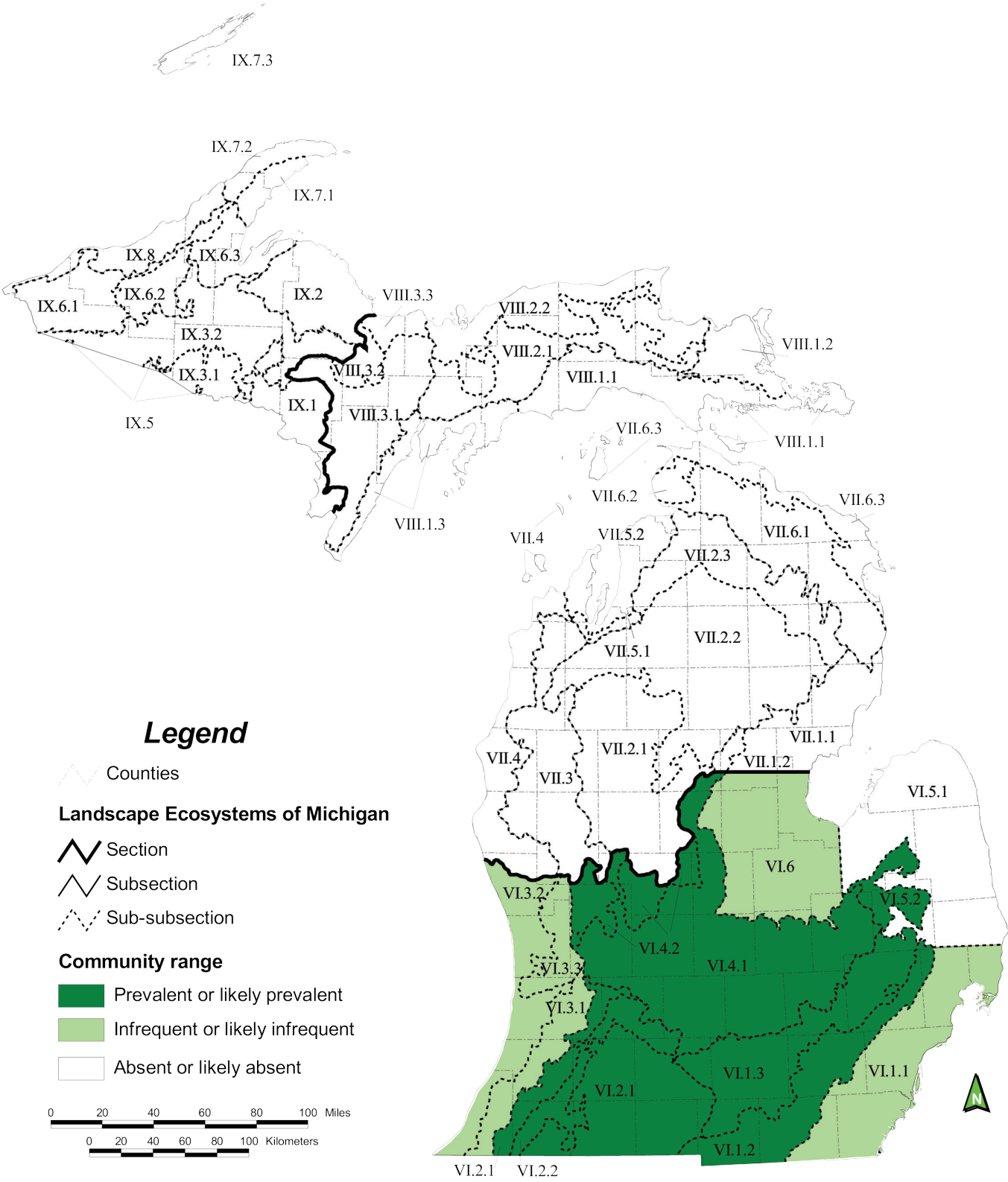**Global and State Rank:** G4/S3 (globally secure/ uncommon in state)

Range: As taxonomic groups, oaks and pines, in the families *Fagaceae and Pinaceae*, respectively, greatly expanded throughout eastern North America during the early Holocene epoch approximately 9,000 to 7,000 years before present (Abrams 2002). Between 6,000 and 4,000 years before present, a shift from pine to oak dominance coincided with a drier climate than before. Also, paleoecological studies have shown a corresponding increase in charcoal found in sediment cores during this period that suggests high incidence of fires (Winkler et al. 1986, Szeicz and MacDonald 1991). Oaks and many of their associated species were ecologically suited to these conditions, and, by the time of European settlement, oak-dominated forests were common in southern New England, the mid-Atlantic region, the Southern Appalachians, southeastern parts

of the Atlantic Coastal Plain, the Midwest, and the Lake States (Abrams 2002).

In the Midwest, oak-hickory forests currently occupy areas of Arkansas, Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, Missouri, Ohio, and Wisconsin (NatureServe 2006). Although southern Lower Michigan was initially included in the beech-maple region by Braun (1950), interpretation of records compiled from General Land Office (GLO) Surveys indicated extensive areas of oak-hickory forests in this region (Brewer et al. 1984, Comer et al. 1995). Recognized as belonging to the Central Interior Region by Comer et al. (2003) and the Central Hardwood Region by Bailey (1997), most counties in Michigan's Region VI (i.e., southern Lower Michigan) (Albert 1995) were historically favorable for development of oak-hickory forests. Region VI occurs south of the climatic tension zone and the highest concentration of oak-hickory forests occurred in subsections VI.1 (Washtenaw), VI.2 (Kalamazoo Interlobate), and VI.4 (Ionia) (Comer et al. 1995). Today, primary old-growth oak-hickory forests are limited in Michigan, but secondary- and tertiary-growth forests as well as oak-hickory forests resulting from fire suppression of oak openings and oak barrens, are adequately represented in the above subsections.

Rank Justification: Frelich (1995) estimated that at the time the GLO completed its systematic survey of the Lake States (Minnesota, Wisconsin, and Michigan),

Legend

Counties

Landscape Ecosystems of Michigan

Section

Subsection

Sub-subsection

Community range

Prevalent or likely prevalent

Infrequent or likely infrequent

Absent or likely absent

0 20 40 60 80 100 Miles

0 20 40 60 80 100 Kilometers

Ecoregional map of Michigan (Albert 1995) depicting distribution of dry-mesic southern forest (Albert et al. 2008)

there were 2,786,700 ha (6,886,086 ac) of primary growth oak-hickory forests. Among these three states currently, only 924 ha (2,283 ac) of primary growth oak-hickory forests remain. The initial logging and land clearing efforts by European settlers destroyed most of these original forests (Abrams 1992, Dey 2002). However, total area of secondary-growth oak-hickory forests greater than 80 years of age is approximately 712,700 ha (1,761,120 ac) (Frelich 1995). Because the oak-hickory forest type spans beyond the Lake States and post-primary growth is readily found throughout the glaciated regions of North America, its global status is considered secure (global rank G4) (NatureServe 2006).

In Michigan, oak-hickory forests, which are formally termed dry-mesic southern forests by Michigan Natural Features Inventory (MNFI) (Kost et al. 2007), represent ecosystem types that fall between dry southern forests (i.e., mixed-oak forests) and mesic southern forests (i.e., beech-maple forests) on a soil moisture and nutrient gradient. Historically, these forests experienced episodic fire events with return intervals that were long enough to allow forest development from more open oak woodlands and savannas but short enough to inhibit colonization of late-successional mesic species (Grimm 1983, Abrams 1992). Prior to European settlement, an estimated 764,318 ha (1,888,671 ac) of dry-mesic southern forests occupied Michigan, which contributed approximately 5% of the state's land area (Comer et al. 1995). Counties with the greatest concentration of dry-mesic southern forests were Washtenaw [63,059 ha (155,822 ac)], Barry [52,453 ha (129,614 ac)], Kent [47,432 ha (117,207 ac)], Jackson [46,184 ha (114,123 ac)], St. Joseph [44,746 ha (110,570 ac)], Ionia [42,248 ha (104,397 ac)], Lenawee [39,363 ha (97,268 ac)], Livingston [37,339 ha (92,267 ac)], Oakland [37,310 ha (92,195 ac)], and Calhoun [36,466 ha (90,109 ac)]. These counties are mostly situated in physiographic systems formed between previously advancing glacial lobes (Farrand and Bell 1982), and this contributed to development of coarse-textured soil, topographic diversity, and a mosaic of dry-mesic southern forests, oak openings and barrens, mesic southern forests, and various wetland ecosystems. Since European settlement, this mosaic of ecosystems has experienced changes in climate and accelerated anthropogenic disturbances in the form of logging, agriculture, grazing, fire suppression, invasive species proliferation, forest fragmentation, and land development. Only 68 ha (168 ac) of primary, old-growth dry-mesic southern forests remain in Michigan today (Frelich 1995). However, total area of secondary-growth oak-hickory forests greater than 80 years of age is estimated to be 191,900 ha (474,195 ac) and is most readily found in Barry, Calhoun, Jackson, Livingston, Oakland, and Washtenaw Counties (Michigan Department of Natural Resources 2000). Additionally, there are currently 44 known element occurrences, encompassing 1,578 ha (3,899 ac), that are tracked by MNFI and considered to have high conservation priority. The S3 rank (uncommon in state) reflects this community's vulnerability to further loss and degradation without appropriate conservation and stewardship efforts.

Physiographic Context: Dry-mesic southern forests occur prominently in Michigan's Region VI, Southern Lower Michigan (Albert 1995). When compared to more northerly regions, Region VI is warmer, has a longer growing season, greater growing season heat sum, greater proportion of night heat sum to total heat sum, lower heat sum prior to last spring frost, and a lower precipitation to potential evapotranspiration ratio throughout the growing season (Albert et al. 1986). The daily maximum temperature in July ranges from 29° to 32°C (84° to 90°F), and the daily minimum temperature in January ranges from -9° to -4°C (16° to 25°F). The mean annual total precipitation is 820 mm (32 in), and winter precipitation is higher in Region VI than elsewhere in Michigan with much of it falling as rain. Dry-mesic southern forests are strongly related to these broad climatic factors. Denton and Barnes (1987) found correlations with the above properties to black oak (*Quercus velutina*) and white oak (*Quercus alba*) distribution throughout the state. These two species are apparently adapted to growing in long, warm summers with warm nights and high water deficits. They are drought tolerant but susceptible to late spring freezes. Their abrupt decrease in abundance with increasing latitude reflects sensitivity to a shorter growing season, lower growing season heat sum, and more frequent frost damage north of the climatic tension zone (Nichols 1968).

Climate determines extent of vegetative communities across large landscapes, but variation in physiography, which accounts for landform, topography, soil, and disturbance dynamics, structures finer-scale distribution patterns (Barnes et al. 1998). Within Region VI, dry-mesic southern forests occur with greatest frequency on coarse-textured end moraines, ice-contact kames, and outwash plains. Additionally, they may be found on sand lake plain, clay lake plain overlain by sand, and protected dune ridges. A common ecological feature of all landforms in which dry-mesic southern forests occur is well-drained to somewhat excessively-drained soil. Loamy sand to sandy loam soil on topography that promotes water movement and drainage are typical. A typical soil profile is shown in Figure 1. Heavier-textured soil can also occur if accompanied by a substantial proportion of coarse fraction (i.e., pebbles and cobbles) or steep slopes, both of which increase drainage. Mor humus formation is common since oak leaf litter, which is comparatively higher in lignin and cellulose concentration than litter of
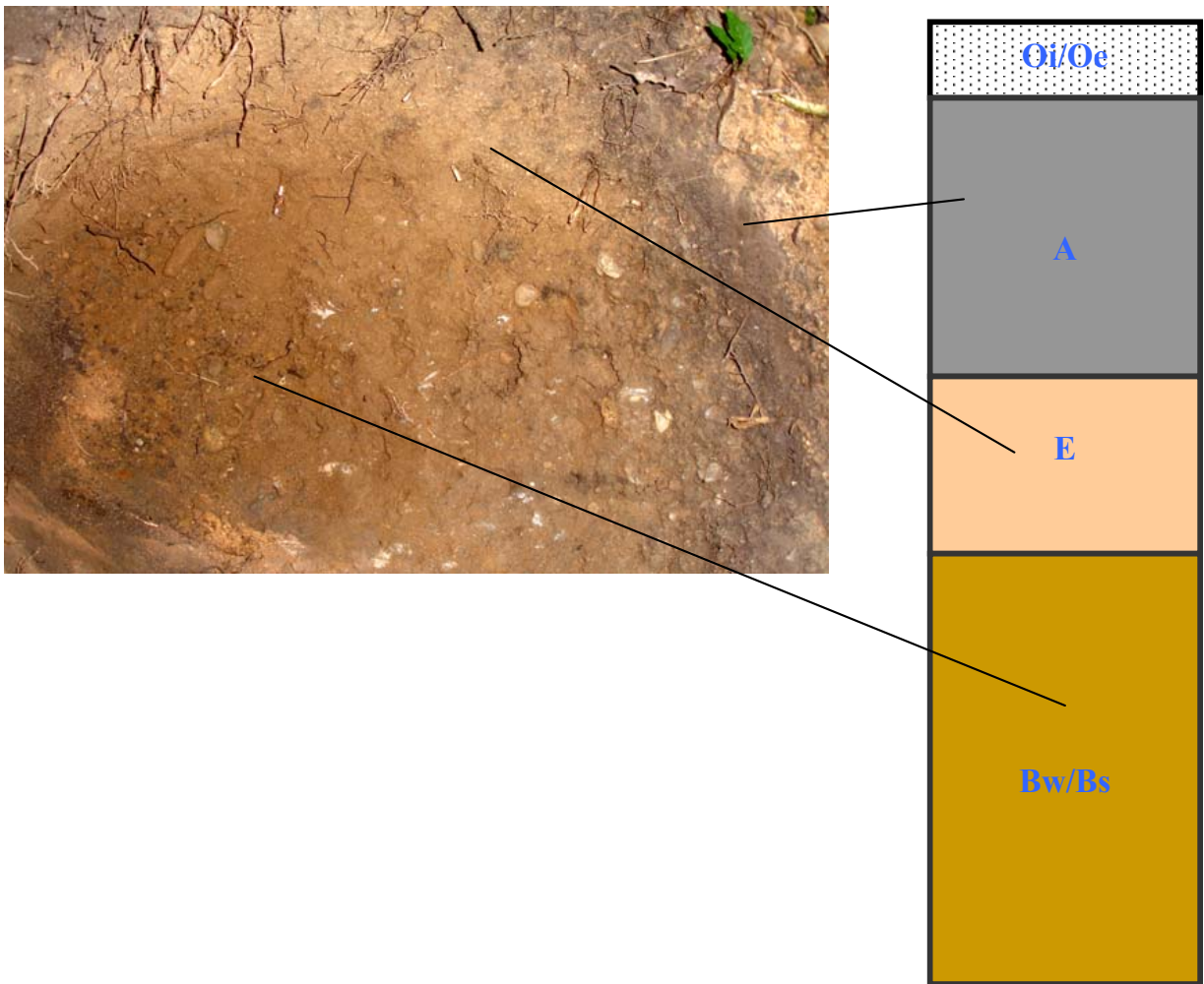
Forest Floor (Litter)

Oi: 4 – 1 cm
Oe: 1 – 0 cm

Mineral Horizons

A: 0 – 20 cm   loam
E: 21 – 32 cm   loamy sand/sandy loam
Bw/Bs: 33 – 100+ cm   loamy sand/sandy loam

Figure 1. Typical soil profile for dry-mesic southern forests showing typical horizon designations, depths, and textures.

mesophytic species, is resistant to decomposition and accumulates on the forest floor (Curtis 1959). Slope percent can range widely, from nearly flat on porous outwash to up to 60% on ice-contact kame slopes with sandy clay loam soil (Lee and Kost 2007, unpublished data). When occurring on high topographic relief, dry-mesic southern forests occupy ridge tops and upper and middle slopes (Curtis 1959, Archambault et al. 1990). Soil pH and total nutrient concentrations (phosphorus, potassium, calcium, and magnesium) of the upper 10 cm A horizon were found to average 4.97 (range 4.25-6.25) and 629 µg/g (range 217-1,707 µg/g), respectively (Lee and Kost 2007, unpublished data) for various oak-dominated sites throughout southern Lower Michigan. In comparison, Kron (1989) reported average values of 6.2 and 1,849.5 µg/g for pH and total nutrient concentrations, respectively, for a sugar maple- (*Acer saccharum*) dominated mesic southern forest on north-facing slopes in southwestern Lower Michigan.

Prior to European settlement, dry-mesic southern forests occurred in a mosaic with other ecosystem types. Because fires strongly influenced patterns of vegetation distribution historically (Abrams 1992), oak forests, woodlands, savannas, and prairies formed a constantly shifting continuum (Cohen 2004a). Each ecosystem type was believed to grade into one another, and boundary location was determined by fire dynamics as affected by fire frequency, fire intensity, and fuel loading and the presence of fire breaks in the form of forested wetlands, water bodies, and changes in topography or edaphic conditions. In the savanna and prairie dominated landscape of southern Lower Michigan, dry-mesic southern forests were typically relegated to locations adjacent to fire breaks, occurring on terraces above river floodplains, along peninsulas in lakes, and juxtaposed next to swamps. Other closed forest types may have also occurred in proximity to dry-mesic southern forests. Mesic southern forests dominated by sugar maple, American beech (*Fagus grandifolia*), or basswood (*Tilia americana*) may have occupied north-easterly aspects that promoted a cool, moist microclimate, while oaks occupied opposing hill sides on south-westerly aspects that facilitated greater solar radiation and frequency of fires. Similarly, dry southern forests dominated by black oak and northern pin oak (*Quercus ellipsoidalis*) would have likely occupied the driest, excessively-drained ridge tops and flat outwash and lake plains that exhibited low nutrient and moisture holding capacity and even greater incidence of fires.

Natural Processes: Dry-mesic southern forests are dependent on regular disturbances for their genesis and persistence. An orderly progression of successional stages, whereby existing plant communities facilitate the dominance of the next community, does not operate

in deterministic fashion nor does a climatic climax exist (Clements 1916). Instead, these forests have been historically impacted by external forces that work in conjunction with the modifying influence of physiography and existing biota.

The development of dry-mesic southern forests today, or during any period for that matter, is intimately related to that of prairies and oak savannas and woodlands. Prairies often burned annually (Cottam 1949), savannas burned on average every 4 to 16 years (Dorney 1981, Wolf 2004), and woodlands formed a transitional state towards dry-mesic southern forests when fire intervals lengthened. Cottam (1949) and Abrams (1996) have suggested that fire effects can determine the abundance of these community types relative to one another on landscapes that seemingly have homogenous topography and soil. It is believed that drought, disease, fire, and to a lesser extent, buffalo grazing, inhibited the invasion and recruitment of woody species in prairies and savannas prior to European settlement. However, it was purposely-initiated fire by Native Americans that had greatest influence upon shaping and maintaining the prairie-savanna-woodland-forest mosaic (Gleason 1913, Day 1953, Dorney 1981). Dry-mesic southern forests would have historically occurred near natural fire breaks such as along eastern edges of stream corridors, along peninsulas in lakes, adjacent to wetlands, and on broken topography typical of end moraines and ice-contact kames. Where fires were allowed to progress along flat terrain and be sustained by fine grassland fuels, prairies and savannas would have been more prevalent.

Upland oaks evolved in relatively dry, fire-prone ecosystems and are characterized by a suite of fire and dry-site adaptations (Crow 1988, Reich et al. 1990, Abrams 1996), including fire-resistant bark, resource allocation to belowground root systems, high photosynthesis to respiration rate ratio, and low water potential thresholds for stomatal closure. Fire has also been shown to increase net photosynthesis and conductance of oaks as a result of enhanced leaf nitrogen concentration (Reich et al. 1990). Reproductively, oaks are dependent on fire to reduce litter that impedes acorn germination, thin out competitive groundcover and understory species, stimulate clonal sprouting, and inhibit the activity of acorn predators and tree pathogens and pests (Courteau et al. 2006). Oak advanced regeneration, defined as understory saplings and seedlings that accelerate growth when released by disturbance (Barnes et al. 1998), contributes to future oak dominance by responding positively to episodic fires. Courteau et al. (2006) provide a more detailed summary of oak life strategies as related to fire.

Other natural disturbances besides fire can perpetuate existing dry-mesic southern forests or cause retrogression of late-successional, maple-dominated forests to oak-dominated forests (Curtis 1959). Gap-phase dynamics producing multi-structured, uneven age stands operate most noticeably in sugar maple- and American beech-dominated mesic southern forests (Cohen 2004b) but also influence succession in dry-mesic southern forests. Canopy gap formation originates through localized stem breakage resulting from wind (Runkle 1982), glaze or ice storms (Lemon 1961), attack by oak wilt fungus (*Chalara quercina*), and episodic defoliation caused by insects such as spongy moth (*Lymantria dispar*). Historically, the now-extinct passenger pigeon (*Ectopistes migratorius*) would have also contributed to the creation of canopy openings. Roosting and nesting activity by thousands of pigeons resulted in stem breakage and the subsequent addition of coarse woody debris to the forest floor, which could have increased fire intensity and frequency (Ellsworth and McComb 2003).

Photo by Jeffrey Lee

Sunlight through the canopy is necessary for oak growth.

Unlike sugar maple and American beech, however, larger gaps are needed by oak species to permit existing advanced regeneration to ascend into the overstory. These larger gaps [i.e., >400 m^2 (>4,306 ft^2)] may be provided by tornado-induced windthrow. Gap size and pre-disturbance understory composition largely determine future overstory composition. Smaller gaps [i.e., 20-100 m^2 (215-1,076 ft^2)] formed in dry-mesic southern forests may slightly increase growth of overstory oaks and hickories or cause accelerated growth of understory red maple (*Acer rubrum*). Conversely, gaps exceeding 400 m^2 (4,306 ft^2) may stimulate recruitment of understory oak species, red maple, white ash (*Fraxinus americana*), bigtooth aspen (*Populus grandidentata*), black cherry (*Prunus serotina*), sassafras (*Sassafras albidum*), or cause

proliferation of brambles (*Rubus spp.*) (Curtis 1959, Runkle 1982, Barnes et al. 1998).

Processes Affected by Anthropogenic Disturbance:
By the latter part of the 19th century, European settlers began to impart a greater presence on the landscape. Land clearing, introduction of grazing cattle and sheep, logging, and long periods of fire suppression have greatly altered vegetation and the interrelated ecological processes. Initial logging of closed-canopy forests and widespread mortality of American chestnut (*Castanea dentata*) from the introduced chestnut blight fungus (*Cryphonectria parasitica*) provided the light and soil resources necessary to stimulate recruitment of oak advanced regeneration (Brewer 1995, Abrams 1996). Similarly, oak grubs in savannas, which had remained in a diminutive growth form due to frequent fires, were allowed to grow and fill canopy gaps when fire was excluded. The combined effects from logging and fire suppression greatly decreased areas of oak openings and barrens (Cohen 2004a) but increased the area of dry-mesic southern forests. Without fire, the profusion of woody growth can succeed to closed-canopy forests within 20 to 40 years (Curtis 1959, Chapman 1984, Crow 1988).

Over time in the absence of fire, oaks and hickories matured and attained overstory dominance. Subsequently, waves of density-dependent mortality occurred through competition of limited understory resources (Barnes et al. 1998) and the spread of oak wilt fungus via proximal root grafting. Surviving understory oaks persisted in the understory for some time, but, due to the longevity of oaks [200-400 years, Barnes and Wagner (2004)], density-independent mortality in the overstory may not have been adequate to allow for necessary light penetration through canopy gaps. Thus, oak sapling recruitment into the overstory would be stalled. Interestingly, oaks have fairly high photosynthetic rates and low to moderate respiration rates in shaded conditions compared to many non-oak species (Abrams 1996). Furthermore, oaks have a low light compensation point (i.e., light level where photosynthetic rate equals respiration rate). All these physiological properties would seem to confer understory tolerance. However, its tolerance only manifests itself as persistence under conditions of episodic disturbance. Allocation of resources to underground reserves and production of defensive phenolic compounds (Abrams 1996) allow oaks to withstand several decades of unfavorable environmental conditions in the understory. When canopy openings occur, especially by fire, belowground reserves are then utilized for accelerated photosynthetic activity and shoot extension. Only when canopy gaps are sufficiently large enough with canopy cover ranging from 25 to 50% (Brose et al. 1999, Hartman et al.

2005), are oaks able to take advantage of their high photosynthesis to respiration rate ratio and recruit quickly into the overstory (Bazzaz 1979). The importance of regular disturbance events to maintain partial canopy openings is emphasized by Hartman et al.'s (2005) findings that oaks poorly regenerate under their own fully developed canopy.

The failure of oaks to recruit into the overstory is not a direct effect of its understory intolerance per se, but rather its competitive disadvantage compared to other shade-tolerant species. Abrams (1996) has cited several studies showing the capability of oaks to respond to release after several decades of suppression. However, conditions for release occurred with limited understory competition and virtually no deer browsing. In today's fire-suppressed dry-mesic southern forests, invasion by shade-tolerant and fire-sensitive species has become ubiquitous. This scenario is especially pronounced on landforms that have soil with relatively high nutrient concentrations and moisture holding capacity (Host et al. 1987). Dry-mesic southern forests on gently-sloping, well-drained moraines and ice-contact landforms with heavy-textured soil are most susceptible to mesophytic invasion. Tall understory vegetation, including native shrubs [e.g., witch-hazel (*Hamamelis virginiana*) and prickly-ash (*Zanthoxylum americanum*)] and non-native shrubs [e.g., autumn-olive (*Elaeagnus umbellata*), Eurasian honeysuckle (*Lonicera spp.*), common buckthorn (*Rhamnus cathartica*), and multiflora rose (*Rosa multiflora*)] and mid- and late-successional trees [e.g., sugar maple, red maple, white ash, basswood, and hop-hornbeam (*Ostrya virginiana*)] can cause substantial reduction in oak seedling survival and growth. Lorimer et al. (1994) found 70% mortality in planted oak seedlings under 97% understory foliar cover during a five-year period. Height growth of surviving oak seedlings averaged only 4 to 6 cm/year (1.6 to 2.4 in/year).

Of all fire-sensitive competitors, greatest attention has been given to red maple (Curtis 1959, Lorimer 1984, Host et al. 1987, Abrams and Nowacki 1992). Red maple exhibits genetic plasticity and adapts to various environmental conditions (Abrams 1998). It competitively displaces oak species in fire-suppressed dry-mesic southern forests because it has higher understory tolerance compared to oaks. Moreover, it is capable of utilizing smaller canopy gaps to recruit into the overstory. When established in the overstory, red maple casts dense shade and produces copious amounts of seed that disperse widely. Germination occurs the same year as dispersal, and multi-structured layers of red maple can form in formerly oak-dominated stands within several decades. Though fire-sensitive at an early age, red maple is persistent and becomes resilient to fire once established in the tall understory. Basal sprout

density was found to increase with each subsequent fire following prescribed burns in Kentucky (Blankenship and Arthur 2006), and additional logging usually accelerates the rate of red maple canopy dominance (Abrams and Nowacki 1992). It has also been suggested that red maple may be capable of producing negative effects on oak nutrient uptake and growth by reducing beneficial mycorrhizal infection of fine oak roots (Dickie et al. 2002).

Lastly, the succession of oak-dominated dry-mesic southern forests to red maple-dominated systems is exacerbated by white-tail deer (*Odocoileus virginianus*) browsing, non-native invasive shrubs, and spongy moth defoliation. Oak regeneration is impacted by these events to a far greater extent than is red maple (Abrams 1998, Sekura et al. 2005). High deer densities may facilitate the spread of non-native species as deer are efficient seed dispersal agents and their hoof prints can provide open microsites for seed germination and seedling establishment. Concerning oak regeneration, deer impose direct negative impact through browsing and indirect negative impact through non-native plant dispersal. Prolific spread of non-native shrubs can competitively exclude oak species by casting dense shade over seedlings, preventing acorn contact with mineral soil, and altering ecosystem processes and soil chemistry. For example, common buckthorn can cause increases in soil nitrogen, carbon, pH, and moisture and modify N mineralization rates (Heneghan et al. 2006). Eutrophication of the ecosystem can further increase deer browse, cause shifts in the composition of vegetation, and lengthen natural fire intervals. If left alone, common buckthorn becomes the dominant ecosystem driver while perpetuating itself and discouraging future oak presence. Courteau et al. (2006) provide a more detailed treatment on deer browsing and oak diseases and pests.

Vegetation Description: There is great difficulty in reconstructing accurate composition of all vegetation layers in dry-mesic southern forests prior to European settlement. General Land Office survey notes accounted for line and corner overstory trees, but understory and groundcover vegetation was not emphasized. Moreover, the rapid expansion of European influence and manipulation of forest lands over a century ago have resulted in significant changes in today's vegetation. Altered disturbance frequencies, introduction of commercial agriculture, intensified grazing and deer browsing, and preferential logging of certain commercially valuable tree species [e.g., northern red oak (*Quercus rubra*) and white oak], have drastically altered the floristic composition and structure of dry-mesic southern forest and skewed the current perception of this system. However, with 44 documented element occurrences and several studies conducted in such

forests, it is possible to provide a representative construct of the vegetation.

Photo by Jeffrey Lee

Invasive species, such as autumn-olive, can form understory shrub tickets in the absence of fire.

The mature overstory is typically dominated by oaks approximately 130 years old and has an average stem density of 442 stems/ha (179 stems/ac) with a range of 300-615 stems/ha (121-249 stems/ac) and a basal area of 35 m²/ha (152 ft²/ac) with a range of 26-41 m²/ha (113-179 ft²/ac). Among oaks, typical average diameter at breast height (dbh) is 43 cm (17 in) with a range of 9-90 cm (4-35 in) (Lee and Kost 2007, unpublished data). Overstory stem density is likely higher today than historically due to a reduction of episodic fire and, therefore, natural thinning. Canopy dominants are white oak, northern red oak, and black oak. Currently, the oldest oaks in most dry-mesic southern forests measure approximately 60 cm (24 in) dbh (Lee and Kost 2007, unpublished data), but these species are capable of attaining diameters greater than 120 cm (47 in) dbh (Barnes and Wagner 2004). Common associates in the canopy and subcanopy include red maple, pignut hickory (*Carya glabra*), shagbark hickory (*Carya ovata*), white ash, hop-hornbeam (restricted to subcanopy), black cherry, and sassafras. Occurring occasionally are sugar maple, bitternut hickory (*Carya cordiformis*), American beech, black walnut (*Juglans nigra*), tuliptree (*Liriodendron tulipifera*), eastern white pine (*Pinus strobus*), bigtooth aspen, trembling aspen (*Populus tremuloides*), basswood, and American elm (*Ulmus americana*).

The understory has a typical average stem density of 1,344 stems/ha (544 stems/ac) with a range of 280-2,020 stems/ha (113-817 stems/ac) and a basal area of 2 m²/ha (9 ft²/ac) with a range of 1-4 m²/ha (4-17 ft²/ac). Among oaks, typical average dbh is 6

cm (2 in) with a range of 2-9 cm (1-4 in) (Lee and Kost 2007, unpublished data). Historically, regular fire events would have thinned out much of the understory. Therefore, today's understory density in dry-mesic southern forests is an inflated depiction. All aforementioned overstory species may be present in the understory, but for oak species, understory abundance is much less than in the overstory. The converse is usually true for species that can asexually reproduce by root suckering or basal sprouting, such as black cherry, bigtooth and trembling aspen, red maple, and sassafras. Past disturbances that have caused canopy openings and mobilization of soil nutrients in conjunction with species-specific reproductive strategies greatly determine understory stem density and composition. Small trees that never attain canopy dominance include Juneberry (*Amelanchier arborea*), flowering dogwood (*Cornus florida*), and choke cherry (*Prunus virginiana*). Tall shrubs include gray dogwood (*Cornus foemina*), American hazelnut (*Corylus americana*), witch-hazel, American fly honeysuckle (*Lonicera canadensis*), maple-leaf viburnum (*Viburnum acerifolium*), downy arrow-wood (*Viburnum rafinesquianum*), and prickly-ash. Low shrubs include bush honeysuckle (*Diervilla lonicera*), ground juniper (*Juniperus communis*), prickly gooseberry (*Ribes cynosbati*), pasture rose (*Rosa carolina*), common blackberry (*Rubus allegheniensis*), northern dewberry (*Rubus flagellaris*), black raspberry (*Rubus occidentalis*), and red raspberry (*Rubus strigosus*). Acidic-shrub indicators that are more commonly found on dry southern forests (i.e. mixed-oak forests) also occur. They include wintergreen (*Gaultheria procumbens*), huckleberry (*Gaylussacia baccata*), and lowbush blueberry (*Vaccinium angustifolium*).

Historically, species associated with oak savannas and prairies would have been well represented in the ground cover of dry-mesic southern forests. Today, however, these species have largely disappeared. Though remnants with residual prairie species exist, current ground cover demonstrates a marked decrease in species richness from the period prior to European settlement. For species lists of oak openings, please see Cohen (2004a). Groundlayer coverage can be highly variable in dry-mesic southern forests. In more mesic ecosystems, dense shade cast by northern red oak, red maple, and sometimes sugar maple, limits ground cover to shade tolerant species. Even in mature dry-mesic forests with a well-developed understory, typical average groundlayer coverage is 9% with a range of 3-25%, and average richness is 6.5 species/m² with a range of 4.3-9.9 species/m² (Lee and Kost 2007, unpublished data). Drier sites with incomplete canopy closure and patchy openings may encourage greater groundcover diversity. Ecologists at MNFI conducted plotless surveys of element

occurrences and found an average of 58 species per site with a range of 10-175 species per site (figures include species from all vegetation strata). The most frequently encountered native species include doll's-eyes (*Actaea pachypoda*), tall agrimony (*Agrimonia gryposepala*), wild sarsaparilla (*Aralia nudicaulis*), jack-in-the-pulpit (*Arisaema triphyllum*) big-leaved aster (*Aster macrophyllus*), rattlesnake fern (*Botrychium virginianum*), Pennsylvania sedge (*Carex pensylvanica*), pipsissewa (*Chimaphila umbellata*), enchanter's-nightshade (*Circaea lutetiana*), squawroot (*Conopholis americana*), poverty grass (*Danthonia spicata*), clustered-leaved tick-trefoil (*Desmodium glutinosum*), naked tick-trefoil (*D. nudiflorum*), wild strawberry (*Fragaria virginiana*), annual bedstraw (*Galium aparine*), white wild licorice (*G. circaezans*), shining bedstraw (*G. concinnum*), hairy bedstraw (*G. pilosum*), fragrant bedstraw (*G. triflorum*), wild geranium (*Geranium maculatum*), white avens (*Geum canadense*), beggar's lice (*Hackelia virginiana*), round-lobed hepatica (*Hepatica americana*), bottlebrush grass (*Hystrix patula*), four-leaved loosestrife (*Lysimachia quadrifolia*), Canada mayflower (*Maianthemum canadense*), hairy sweet-cicely (*Osmorhiza claytonii*), several panic grasses (*Panicum columbianum*, *P. commonsianum*, *P. dichotomum*, *P. implicatum*, *P. latifolium*, *P. meridionale*, and *P. oligosanthes*), Virginia creeper (*Parthenocissus quinquefolia*), downy Solomon seal (*Polygonatum pubescens*), jumpseed (*Polygonum virginianum*), old-field cinquefoil (*Potentilla simplex*), lopseed (*Phryma leptostachya*), May apple (*Podophyllum peltatum*), white lettuce (*Prenanthes spp.*), large-leaved shinleaf (*Pyrola elliptica*), small-flowered buttercup (*Ranunculus abortivus*), black snakeroot (*Sanicula gregaria*), false spikenard (*Smilacina racemosa*), bristly green-brier (*Smilax tamnoides*), blue-stemmed goldenrod (*Solidago caesia*), early meadow-rue (*Thalictrum dioicum*), poison-ivy (*Toxicodendron radicans*), common trillium (*Trillium grandiflorum*), bellwort (*Uvularia grandiflora*), several violets (*Viola canadensis*, *V. pubescens*, *V. sagittata*, and *V. sororia*), summer grape (*Vitis aestivalis*), and riverbank grape (*V. riparia*).

Non-native invasives that have become problematic in dry-mesic southern forests include garlic mustard (*Alliaria petiolata*), Japanese barberry (*Berberis thurbergii*), Oriental bittersweet (*Celastrus orbiculata*), spotted knapweed (*Centaurea maculosa*), autumn-olive, Amur honeysuckle (*Lonicera maackii*), Morrow's honeysuckle (*Lonicera morrowii*), Tartarian honeysuckle (*Lonicera tatarica*), Canada bluegrass (*Poa compressa*), Kentucky bluegrass (*Poa pratensis*), common buckthorn, and multiflora rose. Species lists were compiled from Lee and Kost (2007) and MNFI database, and nomenclature follows Voss (1972, 1985, and 1996).

Other Noteworthy Species: Several rare plants and animals are known to be found in dry-mesic southern forests. MNFI recognizes 43 rare species (Tables 1 and 2). Additionally, many common wildlife species utilize the habitat afforded by dry-mesic southern forests and rely on the production of acorn masts [see Courteau et al. (2006) for complete lists].

Conservation and Biodiversity Management: From a conservation perspective, large contiguous areas of dry-mesic southern forests occurring in a matrix with intact dry southern forests, oak barrens, oak openings, mesic southern forests, and wetland pockets should have priority. Limiting fragmentation, and therefore edge disturbance, is crucial to retarding and preventing the colonization of invasive species and maintaining interior-dependent wildlife populations. Unfortunately, dry-mesic southern forests occur in the highly-developed southern part of Michigan. Development and agriculture have greatly reduced total forest area to mostly isolated pockets within state game areas, state parks, state recreational areas, and smaller county and municipal parks. High-quality, remnant dry-mesic southern forests do occur on private lands, and landowner outreach and education is pivotal to ensure future conservation. Federal assistance in the form of the Landowner Incentive Program is an excellent example of how researchers, Department of Natural Resources and extension specialists, and private stakeholders can coordinate activities aimed at preserving privately-owned forest lands.

Today, the more salient issue for foresters and wildlife biologists is management, rather than protection of dry-mesic southern forests. There are economic, recreational, wildlife, and biodiversity implications related to succession of such forests to those characterized by late-successional, mesophytic species. Decades of fire suppression have changed ecosystem functions in dry-mesic southern forests. Flammable oak litter with high lignin content is now replaced by more readily decomposable maple litter, which lowers the likelihood of recurring surface fires. As more shade-tolerant species, especially red maple, become more prevalent in the understory and overstory, conditions become conducive for self-perpetuation of shade-tolerant species to the detriment of oak regeneration (Abrams 2005). Furthermore, increased deer density beyond historic levels (Strole and Anderson 1992, Fredericksen 1998) and the possibility of insect and pathogen outbreaks are compounding factors that must be addressed if there is desire to sustain dry-mesic southern forests in the future.

Oak-dominated ecosystems on very dry sites are relatively easy to manage for sustainable oak regeneration. For example, edaphic controls (i.e., low

Table 1. Rare plant species associated with dry-mesic southern forests.

Scientific Name	Common Name	State Status*
Agrimonia rostellata	beaked agrimony	SC
Arabis missouriensis var. *deamii*	Missouri rock-cress	SC
Aristolochia serpentaria	Virginia snakeroot	T
Baptisia leucophaea	cream wild indigo	E
Castanea dentata	American chestnut	E
Celtis tenuifolia	dwarf hackberry	SC
Dennstaedtia punctilobula	hay-scented fern	T
Eupatorium sessilifolium	upland boneset	T
Geum virginianum	pale avens	SC
Houstonia caerulea	bluets	X
Linum virginianum	Virginia flax	T
Liparis liliifolia	purple twayblade	SC
Phlox ovata	wideflower	E
Quercus shumardii	Shumard's oak	SC
Scutellaria elliptica	hairy skullcap	SC
Silene stellata	starry campion	T
Silene virginica	fire pink	E
Triphora trianthophora	three-birds orchid	T
Viburnum prunifolium	black haw	SC

* E, Endangered; T, Threatened; SC, Special Concern; X, Extirpated

Table 2. Rare faunal species associated with dry-mesic southern forests.

Taxonomic Group	Scientific Name	Common Name	State Status
Amphibians			
	Ambystoma opacum	marbled salamander	T
Birds			
	Buteo lineatus	red-shouldered hawk	T
	Dendroica cerulea	Cerulean warbler	T
	Wilsonia citrina	hooded warbler	SC
Insects			
	Battus philenor	pipevine swallowtail	SC
	Catocala dulciola	quiet underwing	SC
	Catocala robinsoni	Robinson's underwing	SC
	Erynnis baptisiae	wild indigo duskywing	SC
	Fixsenia favonius ontario	northern hairstreak	SC
	Neoconocephalus retusus	conehead grasshopper	SC
	Nicrophorus americanus	American burying beetle	X
	Oecanthus pini	pinetree cricket	SC
	Papaipema cerina	golden borer	SC
	Pygarctia spraguei	Sprague's pygarctia	SC
Mammals			
	Microtus pinetorum	woodland vole	SC
Reptiles			
	Clemmys guttata	spotted turtle	T
	Emydoidea blandingii	Blanding's turtle	SC
	Nerodia erythrogaster neglecta	copperbelly watersnake	E
	Pantherophis spiloides	gray ratsnake	SC
	Sistrurus catenatus catenatus	eastern massasauga	SC
Snails			
	Anguispira kochi	banded globe	SC
	Mesomphix cupreus	copper button	SC
	Vallonia gracilicosta albula	land snail	SC
	Xolotrema denotata	velvet wedge	SC

* E, Endangered; T, Threatened; SC, Special Concern

soil moisture and nutrient levels, highly leached acidic soil, and wind-induced erosion and desiccation) prevent mesophytic invasion in excessively-drained outwash plains in Michigan (Host et al. 1987, Archambault et al. 1990), xeric ridges in the unglaciated Ozarks of Arkansas, and Appalachian oak forests of Virginia (Pallardy et al. 1998). In the younger and more nutrient-rich, glaciated soil of southern Michigan, the dry-mesic southern forests likely developed under a historic fire regime that favored oaks and hickories to the exclusion of mesophytic shade-tolerant species. Without this disturbance, edaphic conditions would have permitted succession towards more shade-tolerant species such as red maple, sugar maple, and American beech. Consequently, today's management strategy must be centered on prescribed burning, understory removal of competitive species and non-native shrubs, and control of deer browse and insect and pathogen outbreaks.

Managing for oak regeneration through cutting, prescribed fire, application of herbicides, or some combination of several techniques has been difficult and inconsistent. Successful oak regeneration requires release and recruitment of understory oaks relative to competing species. Sander et al. (1976) concluded that at least 1,063 stems greater than 137 cm (4.5 ft) in height of oak advanced regeneration per hectare (430 stems/ac) were needed prior to a clearcut harvest to produce a pole stand containing 30% oak. Rarely, however, does advanced regeneration approach this density in dry-mesic southern forests of Michigan. More common are scattered seedlings under 50 cm (20 in) in height and little representation in the understory or subdominant overstory. Clearcutting under such conditions results in colonization of early-successional, shade-intolerant individuals such as bigtooth aspen, black cherry, and sassafras or promotes vigorous sprouting of existing shade-tolerant species (Abrams and Nowacki 1992). Though oaks are capable of producing coppice sprouts, growth rates are generally subordinate to clonal sprouting of competitors.

Shelterwood harvests have been utilized as an alternative to clearcutting on more productive sites with some success (Loftis 1990, Brose et al. 1999). Residual oak trees are left in the overstory to moderate the understory microclimate, provide regenerative seed mast, and to allow for enough shade to discourage shade-intolerant species growth. Timing of shelterwood cuts should coincide with acorn crops and at least 20% full sunlight is needed for positive rates of shoot growth for black oak and northern red oak (Gottschalk 1994). Unfortunately, the same conditions created by a shelterwood cut that are favorable for oak also apply to black cherry and red maple. In fact, both species exhibit higher plasticity than oaks to adjust leaf weight to leaf

area ratio in changing light conditions (Gottschalk 1994). This translates into adaptable crown response to shelterwood cuts that may place oaks at a competitive disadvantage when growing with abundant black cherry and red maple seedlings and saplings.

Photo by Michael Kost

Coppice sprouting of black oak.

Success of silvicultural treatments for the purpose of oak regeneration in dry-mesic southern forests relies on understory control of mesophytic species (Hill and Dickmann 1988). There are promising results when herbicide is applied to competing vegetation prior to cutting (Johnson et al. 1989). Bundy et al. (1991) simultaneously removed competing vegetation while exposing the mineral seedbed for oak germination by scarifying the soil. A similar treatment involves mechanical uprooting of larger-stemmed competitors (Jacobs and Wray 1992). The resilience of oaks to mechanical removal is enabled by their deep taproots and ability to sprout following top injury. Less intrusive and ecologically sensitive alternatives are hand-felling and girdling of competitors in conjunction with herbicide application to stumps. Many of these methods, though somewhat effective, can be economically feasible only on a small scale. Chemicals used in herbicides are costly, and targeted species-specific spraying is laborious. Compaction and disintegration of soil structure often are indirect effects when attempting mechanical removal, and soil disturbance can greatly increase invasive species populations that are present prior to treatment. Consequently, the most widely practiced method of understory species control is prescribed burning in combination with overstory thinning.

With a well-established understory, low to moderate intensity burns conducted at infrequent intervals are ineffective in removing competing species or encouraging oak regeneration (Stan et al. 2006).

Blankenship and Arthur (2006) found reduced stem density of red maple in the Appalachian oak ridges of Kentucky following three, low-intensity, surface burns in a five-year period. However, oak abundance was negatively affected and the mean number of sprouts per stem of red maple actually increased following treatment. By contrast, a study in northeastern Ohio, found that five successive annual burns following understory thinning encouraged oak species regeneration (Sekura et al. 2005). In the Piedmont of Virginia, a single, high-intensity spring fire conducted 2 to 4 years following a 50% basal area reduction shelterwood cut was sufficient to regenerate oak to 75% dominance (Brose et al. 1999). Brose et al. (1999) also indicated that medium-high-intensity burns during the spring or winter will result in dominance by oaks and mesophytic species in roughly equal proportions. Low intensity burns, however, will result in strictly mixed-mesophytic dominance.

Photo by Jeffrey Lee

Heavy mesophytic understory following thinning.

The success of prescribed burns in conjunction with other management strategies in promoting oak regeneration is highly dependent on local ecosystem characteristics. Franklin et al. (2003) concluded that each ecosystem responds according to extant species at the time of treatment. In other words, initial condition of the ecosystem prior to disturbance largely determines the outcome of post-treatment succession. After more than a century of fire suppression and anthropogenic disturbance, succession within Michigan's dry-mesic southern forests now gravitates towards greater mesophytic dominance. Understory stems greater than 4 cm (2 in) dbh of fire-sensitive species become robust enough to survive low- to medium-intensity fires (Franklin et al. 2003), and, therefore, restoration of dry-mesic southern forests to conditions that will allow for self-perpetuation of oaks requires long-term, sustained investment of management resources.

Additional considerations for managing dry-mesic southern forests involve deer, and non-native invasive shrubs, herbs, insects, and pathogens. Controlling deer browse is problematic when deer density is high, so annual culling is necessary. As a silvicultural practice, leaving residual slash piles after logging can serve as a physical deterrent to deer intrusion in a restoration area. It is imperative to protect oak seedlings and saplings from overbrowsing, and, on a small scale, protective exclosures may be used. Early-successional forests tend to attract deer because low hanging branches and shrubs provide easy forage. Managing for mature forests by lengthening logging rotations and discouraging forest fragmentation will attract less deer. Additionally, diversifying the understory and ground cover layers with oak forest species (e.g., through artificial seeding of native species) may alleviate oak browsing pressure. Though deer do have a slight preference for oaks, they are also generalists capable of browsing many plant species (Strole and Anderson 1992).

Non-native invasive shrubs and herbs can be just as problematic for oak regeneration as competition from native mesophytic species. In most cases, non-native species can be controlled alongside other targeted species, such as red maple. Mechanical removal and prescribed fire is a common approach, but, in more severe situations, herbicidal treatment may be necessary. Because non-native invasive shrubs and herbs have the potential to alter ecosystem processes (Heneghan et al. 2006), restoration of dry-mesic southern forests that have sustained, long-term presence of non-native species must take into account potential legacy effects. For instance, elevated soil nitrogen levels may remain in an ecosystem for some time following removal of common buckthorn, and garlic mustard rhizosphere leachates can disrupt mutualisms between native vegetation and mycorrhizae (Roberts and Anderson 2001, Stinson et al. 2006). Such legacies impact objectives for native plant restoration, and the duration of residual effects likely varies with different non-native species.

Prevention of insect and pathogen outbreaks is best approached by maintaining low stem densities, which is both conducive to oak regeneration and inhibitory to density-dependent spread of potential infections. Forest stands with low overstory density and high overstory diversity may retard oak wilt spread (O'Brien et al. 2000). Also, closely spaced trees are known to experience root grafting and can transmit resources among one another in mutualistic fashion. This is likely facilitated by mycorrhizal fungi (Dickie et al. 2002), but pathogenic outbreaks may also be spread more easily by this same mechanism. Therefore, it is prudent to maintain growing conditions that encourage oak regeneration, species diversity, and restrict the severity of insect and pathogenic outbreaks should they occur. As previously stated, dry-mesic southern forests

historically formed a matrix along with oak woodlands, oak savannas, and prairies. Former oak savannas that have converted to closed canopy oak systems due to fire suppression are prevalent in Michigan's landscape. Since dry-mesic southern forests provide habitat for forest-dwelling species, such as Neotropical migrant birds, conservationists must weigh the costs and benefits of savanna restoration by way of retrogressive conversion from closed oak systems. Increased fragmentation and edge effects may be accompanied by shifts in biota composition and possible non-native species invasion. Savanna remnants selected for restoration should be large in size, with good landscape context (i.e., adjacent to high-quality natural communities), and have a high probability of success. For instance, dry-mesic southern forests that possess ground flora indicative of oak savannas may be good candidates for restoration to a more open canopy state. Cohen (2004a) provides a more detailed discussion concerning the dilemma and implications associated with oak savanna restoration.

Photo by Jeffrey Lee

Open growing conditions promote a spreading-limb growth form.

Research Needs: The most pressing need for managers of dry-mesic southern forests centers around oak regeneration and the rapid increase in dominance of mixed mesophytic species. Much work has already been accomplished investigating the effects of specific management techniques on localized sites. However, developing general management guidelines that are applicable in all situations across a wide array of ecosystems have not been successful. Detailed ecosystem studies incorporating previous management practices and land use history are foundations upon which one can evaluate oak regeneration systematically. Isolating principal variables that contribute to oak regeneration while controlling for certain factors (i.e., soil nutrient concentrations, burning intervals, invasive species abundance, deer browse pressure, stand age, slope position, and aspect) is crucial to understanding the mechanisms driving succession towards or away from the current overstory composition.

Though it is understood that episodic fire was an important disturbance, an accurate description of fire dynamics for dry-mesic southern forests is lacking. Future work must address the historic range of variability in regards to fire return interval, rotation, frequency, intensity, and severity. Increasingly, the use of prescribed fire has been popular for restoration and reintroduction of regular disturbances. Unfortunately, few long-term studies are available that involve prescribed burns conducted regularly over multiple decades. Current dry-mesic southern forests have been disproportionately shaped by decades of fire suppression in comparison to the relatively recent restoration efforts, which are just now beginning to affect change. Continued monitoring and adaptive management based on new findings is advisable.

Finally, from a global change perspective, there is much uncertainty regarding oak ecosystems response to increases in atmospheric CO_2 concentration, nitrogen deposition, carbon source/sink relations, and climate change. Predicted drier conditions and greater incidence of drought in certain regions may actually be beneficial for dry-mesic southern forests (Iverson and Prasad 2001). It is difficult to forecast such events accurately, but such factors should be considered for study. Researchers, forest managers, and restoration workers should be cognizant of their impact.

Similar Communities: Dry-mesic northern forest, dry southern forest, lakeplain oak openings, mesic southern forest, oak barrens, oak openings, oak-pine barrens, and pine barrens.

Other Classifications:

Michigan Natural Features Inventory (MNFI) Circa 1800 Vegetation: White Oak, Black Oak, Hickory Forest (4122)

Michigan Department of Natural Resources (MDNR): O - Oak

Michigan Resource Information Systems (MIRIS): 412 (Central Hardwood), 41207 (Undifferentiated Oak/Hickory), 41214 (Red Oak), 41227 (White Oak), and 41235 (Black Oak)

The Nature Conservancy National Classification:

CODE; ALLIANCE; ASSOCIATION; COMMON NAME

I.B.2.N.a; *Quercus alba - (Quercus rubra, Carya spp.*) Forest Alliance; *Quercus alba - Quercus rubra - Carya ovata* Glaciated Forest; White Oak - Northern Red Oak - Shagbark Hickory Glaciated Forest; Midwestern White Oak - Red Oak Forest

I.B.2.N.a; *Quercus rubra - (Acer saccharum)* Forest Alliance; *Quercus rubra - Quercus alba - (Quercus velutina, Acer rubrum) / Viburnum acerifolium* Forest; Northern Red Oak - White Oak - (Black Oak, Red Maple) / Mapleleaf Viburnum Forest; Northern Red Oak - White Oak - (Maple) Forest

I.B.2.N.a; *Quercus velutina - Quercus alba - (Quercus coccinea)* Forest Alliance; *Quercus velutina - Quercus alba - Carya (glabra, ovata)* Forest; Black Oak - White Oak - (Pignut Hickory, Shagbark Hickory) Forest; Black Oak - White Oak - Hickory Forest

Related Abstracts: Bur oak plains, dry northern forest, dry-mesic northern forest, lakeplain oak openings, mesic southern forest, oak barrens, oak openings, oak-pine barrens, and pine barrens.

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