Description of Vegetation of the Oak Openings of Northwestern Ohio at the Time of Euro-American Settlement[1]

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ABSTRACT. Original land survey notes were used to produce a map of the Oak Openings of northwestern Ohio showing the vegetation at the time of Euro-American settlement (1817-1832). For that period, the area of the Oak Openings was 43% Oak Savanna, 27% Wet Prairie, 23% Oak Woodland, 7% Oak Barrens, and <1% Floodplain Forest. The composition of the tree layer was determined from analysis of records of bearing and line trees recorded by the land surveyors. The tree layer of each of the four major vegetation types was dominated by *Quercus alba*, with *Q. velutina* as a subdominant. *Quercus palustris* was also a subdominant in Oak Barrens and Wet Prairie. Tree density averaged 90 trees/ha in Oak Woodland, 14 in Oak Savanna, 2 in Oak Barrens, and <1 in Wet Prairie. The composition of the shrub and herb layers was estimated based primarily on the literature of the region and our own field research.

Today most stands of the four major vegetation types have been eliminated by urbanization and agriculture, or have changed to forests as tree densities increased with the absence of fire and increased soil drainage. Extant Oak Savannas and Oak Woodlands are different in composition from those present at Euro-American settlement.

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INTRODUCTION

The Oak Openings includes an area of 476 km^2 of sandy soils in Lucas, Fulton, and Henry counties of northwestern Ohio. Scattered areas similar to the Oak Openings can also be found on sandy soils in several counties of southeastern Michigan (Comer and Albert 1998). Prior to Euro-American settlement, Ohio's Oak Openings was surrounded by Black Swamp Forest (Gordon 1966, 1969; Anderson 1992). The Oak Openings is located on sand laid down along the edges of former glacial lakes Wayne, Warren, and Lundy by longshore currents from Michigan. When first formed, the sand beaches were bare and fairly level, but as water levels dropped the wind formed low dunes (Forsyth 1959, 1968; Hehr 1970). The most extensive dune building occurred with Lake Warren, which had the highest elevation (207 m) of the three glacial lakes.

Oak Savannas developed on dune ridges and Wet Prairies formed in interdunal areas (Sears 1926; Moseley 1928; Transeau 1935, Gordon 1966, 1969; Hehr 1970). Drainage was impeded by a clay lakebed 3.0 to 15 m below the sandy surface, so water often covered the Wet Prairies during the winter and spring (Mayfield 1969). By late summer, these wet areas dried and were burned by lightning and human-set fires.

Drainage, agriculture, urbanization, and cessation of fires resulted in significant changes in the vegetation of the region following Euro-American settlement (Mayfield 1969). Nevertheless, the Oak Openings is still of great botanical interest. The combinations of dry and wet habitats, loose sand and black muck soils, and forested and open vegetation have produced an unusual flora. In fact, there are presently 145 state potentially threatened, threatened, and endangered plant species in the Oak Openings, more than any other area in Ohio (McCance and Burns 1984; ODNR 2002a,b; Walters 2003). Kitty Todd Preserve (253 ha) has 88 of these plant species, along with 23 state listed animals (Haase 2003). Many of these plants are common in the northern Great Lakes and Canada (Easterly 1979). Others are western and Atlantic Coastal Plain disjuncts.

Sears (1926) was the first to map vegetation in the Oak Openings, showing the approximate location of a few Wet Prairies and a few open oak areas. Transeau (1935) also mapped prairies in the Oak Openings. Moseley (1928) mapped the boundaries of the Oak Openings but delineated no vegetation types. Gordon (1969) mapped the pre Euro-American settlement boundaries of the Oak Openings but did not map the different vegetation types. Hehr (1970) mapped pre Euro-American settlement boundaries and included locations of Wet Prairies. He also determined the tree composition of the oak-dominated areas but did not separate Oak Forest, Oak Savanna, and Oak Barrens. The objective of this project was to improve on these earlier studies by producing a vegetation map and accompanying text with information on the area, distribution, and composition of the vegetation types in the Oak Openings at the time of Euro-American settlement.

MATERIALS AND METHODS

Description of Surveyors' Notes

Records of the US General Land Office Survey were used to produce a map of the vegetation of the Oak Openings as it existed in 1817-1832 (copies of the surveyors' original field notes are in the Office of the State Auditor in Columbus, OH). The original land parcels in Ohio were defined using the US Rectangular Survey System of township and range in which each township was subdivided into 1.0 mile (1.6 km) square sections.

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Although description of the vegetation was not the surveyors' main objective, they were required to gather specific data related to vegetation. These data included identification of two bearing trees at each section corner; two bearing trees halfway between these corners (that is, at quarter-section points); two bearing trees at points where survey lines entered and left rivers, lakes, or Native American reservations; and trees located directly on survey lines. The surveyors recorded the common name and diameter for each of these trees, as well as distance from the survey point for each bearing tree. In addition, surveyors usually described crossing boundaries of wet prairies, floodplain bottomlands, and various types of swamps or beech-maple forests in the areas surrounding the Oak Openings. Borders of oak savannas were mentioned only occasionally. The surveyors also described the general quality of timber and soil as well as density of undergrowth.

The potential for bias in land survey notes has been noted by Bourdo (1956) and Hushen and others (1966). However, we found no evidence of bias in selection of species for bearing or line trees, except that successional trees such as *Populus tremuloides* (quaking aspen) and *Sassafras albidum* (sassafras) were likely underrepresented because the surveyors were instructed to select trees no smaller than 5.0 in (12.7 cm) dbh (Bourdo 1956). Also, close correlation between the surveyors' records of vegetation boundaries and present day topographical features indicates that the surveyors were accurate.

Classification of Vegetation Types

We focus on five vegetation types: Oak Woodland, Oak Savanna, Oak Barrens, Wet Prairie, and Floodplain Forest. Oak Savanna on sand dunes and Wet Prairie in interdunal swales have long been recognized as vegetation types in the Oak Openings, but we included a) Oak Woodland to recognize areas protected from fire that had greater tree density than Oak Savanna, b) Oak Barrens for areas intermediate in tree density between Oak Savanna and Wet Prairie, and c) Floodplain Forest. Uncommon vegetation types such as sand prairie were not included.

Definition and Delineation of Vegetation Types

We used several methods to delineate vegetation boundaries. Foremost was calculation of tree density based on distances to bearing trees (Anderson and Anderson 1975). Section and quarter-section points were defined as having Oak Woodland vegetation where the mean distance from points to bearing trees was 50 links (10.5 m), Oak Savanna where 50-192 links (10.5-38.8 m), Oak Barrens where 193-333 links (38.8-66.9 m), and Wet Prairie where >333 links (>66.9 m). These distances correspond to density values of >43 trees/ha for Oak Woodland, 4-43 for Oak Savanna, 1-3 for Oak Barrens, and <1 for Wet Prairie. Our density values for defining Oak Woodland, Oak Savanna, and Wet Prairie are similar to those used by Curtis (1959), Anderson and Anderson (1975), and Whitney and Steiger (1985). Our Oak Barrens vegetation type corresponds to low density savanna and high density prairie in these other studies. Where different density values occurred in a small area of several km^2, we calculated the percentages of Oak Woodland, Oak Savanna, Oak Barrens, and Wet Prairie and mapped the area as the most abundant vegetation type (usually only two vegetation types were present in these small areas). Because so few bearing trees were found in the Floodplain Forest, no attempt was made to determine the density of the trees in this vegetation type.

Another important method to delineate vegetation boundaries involved references in surveyors' notes. For example, "post and mound in open plains or prairie" indicated Wet Prairie. Also, surveyors frequently described crossing boundaries of Wet Prairie and Floodplain Forest. Comments by the surveyors at the end of each mile were also helpful, for example, "first 1/2 mile oak woods — second 1/2 mile poor oak plains." In many cases they also listed the dominant species in the canopy and undergrowth, for example, "timber black oak and white oak — undergrowth hazle [that is, hazel], sassafras, whortleberry, fern, wintergreen."

We also used topography as an indicator of vegetation, as Wet Prairies occurred on flat terrain and Oak Savannas on dune ridges. In addition, boundaries of Floodplain Forest often matched abrupt elevation changes of >1.0 m (and were noted in surveyors' descriptions).

Vegetation boundaries were drawn on 7.5-minute series USGS topographical maps. Data were then entered into an ArcView Geographic Information System (GIS) to produce the map.

Description of Vegetation Types

We described tree composition of the different vegetation types based on a) land survey data for bearing and line trees, b) lists of trees given by the surveyors at the end of each line, c) surveys by Edwin Moseley in 1897-1927 (Moseley 1928), and d) our own field research in 1988-1994. We determined diameter size class distributions, relative densities, and average diameters of trees for each species in each vegetation type. Tree species that had not been differentiated by the land surveyors, such as some *Quercus* and *Fraxinus* spp., were separated for our qualitative description of vegetation types based on Moseley's (1928) and our own surveys of the Oak Openings. For example, surveyors did not differentiate *Quercus palustris* (pin oak), *Q. coccinea* (scarlet oak), and *Q. ellipsoidalis* (northern pin oak) from *Q. velutina* (black oak), nor *Q. bicolor* (swamp white oak) from *Q. alba* (white oak).

The surveyors recorded little information on shrubs and herbaceous plants. Therefore, we projected the composition of these layers based primarily on Edwin Moseley's surveys (Moseley 1928), but also on more recent works by Easterly (1969, 1972, 1973, 1979), Anderson (1971, 1992), Tryon (1973), Tryon and Easterly (1975), Hawkins (1977), Walters (2003), and ourselves. To aid in determining which vegetation types (Oak Woodland, Oak Savanna, and so forth) contained which species, we used additional lists from the Midwest

(Curtis 1959; Pruka 1995; Cochrane and Iltis 2000; Bader 2001), as well as studies that placed species along light gradients (Bray 1958; Pruka 1994; Leach 1996; Leach and Givnish 1999; Swenson 1999; Hausman 2001).

Scientific nomenclature follows Gleason and Cronquist (1991).

VEGETATION TYPES

Oak Woodland

Composition: Oak Woodland consisted of stands with tree crowns close but usually not touching, and included sparse forests. Stands averaged 90 trees/ha and were dominated by *Quercus alba*, followed by *Q. velutina* (Table 1). Other tree species included *Acer rubrum* (red maple), *Amelanchier arborea* (serviceberry), *Prunus serotina* (black cherry), *Q. bicolor*, *Q. coccinea*, *Q. ellipsoidalis*, *Q. macrocarpa* (bur oak), *Q. palustris*, and *Sassafras albidum* (all species lists in this section have species in order of declining expected abundance, except where species are arranged alphabetically because relative abundances cannot be estimated). Shrubs were *Aronia prunifolia* (chokeberry), *Gaylussacia baccata* (black huckleberry), *Hamamelis virginiana* (witch hazel), *Malus coronaria* (American crab), *Prunus virginiana* (choke cherry), *Rosa carolina* (pasture rose), *Vaccinium angustifolium* (early low blueberry), and *V. pallidum* (late low blueberry).

The most abundant herbaceous species were *Carex pensylvanica* (early sedge) and *Pteridium aquilinum* (bracken fern). Other herbs included *Anemone quinquefolia* (wood anemone), *Aralia nudicaulis* (wild sarsaparilla), *Aster oolentangiensis* (sky blue aster), *Fragaria virginiana* (wild strawberry), *Gaultheria procumbens* (wintergreen), *Geranium maculatum* (wild geranium), *Helianthus divaricatus* (woodland sunflower), *Lysimachia quadrifolia* (whorled loosestrife), *Osmorhiza claytoni* (sweet cicely), *Polygonatum biflorum* (smooth Solomon's seal), *Potentilla simplex* (old-field five-fingers), *Rubus flagellaris* (dewberry), *Smilacina racemosa* (false Solomon's seal), *Solidago rugosa* (rough stemmed goldenrod), and *Viola sororia* (common blue violet).

Comments: Oak Woodland formerly covered 107 km^2 (23%) of the Oak Openings (Fig. 1). It was most common in areas that offered partial protection from fire, such as along the perimeter of the Oak Openings, near streams, and near topographic changes (although changes in elevation were generally only 1-3 m; Forsyth 1968; Hehr 1970). Fires presumably moved from west to east following prevailing winds, except when storms came from the east across Lake Erie. Similar site factors have been identified as affecting the distribution of vegetation elsewhere in the Midwest (Grimm 1984; Whitney and Steiger 1985; Leitner and others 1991; Will-Wolf and Montague 1994). Fires were probably less frequent and less intense than in the other oak-dominated vegetation types, but nevertheless kept tree density below the 155 trees/ha of the nearby Black Swamp Forest.

All Oak Woodland was cleared for agriculture following Euro-American settlement, but the poor sandy soils resulted in many areas being abandoned and reverting to Woodland. With the lack of fire, tree densities increased and Oak Savanna converted to Oak Woodland; today there is more Oak Woodland in the Oak Openings than before Euro-American settlement, despite considerable urbanization of the northern Oak Openings. However, the Oak Woodland changed from *Quercus alba* to *Q. velutina* dominance (unpublished data). Moreover, without fire many Oak Woodlands (and Oak Forests) changed in composition as less fire-resistant species such as *Prunus serotina*, *Acer rubrum*, and *Sassafras albidum* increased in abundance. With increased shade and leaf litter, there has been a dramatic reduction in oak regeneration, as well as reduced diversity and abundance of shrubs and herbs (especially *Gaultheria procumbens*, whose reduction also may be related to the loss of topsoil).

Oak Savanna

Composition: Oak Savanna, with an average of 14 trees/ha, was much less dense than Oak Woodland. Stands were dominated by *Quercus alba* and *Q. velutina* (Table 1), but included *Q. palustris*, *Q. coccinea*, *Q. ellipsoidalis*, *Populus tremuloides*, and *Prunus serotina*. Dominant shrubs included *Vaccinium pallidum*, *V. angustifolum*, *Gaylussacia baccata*, and *Rhus copallina* (dwarf sumac). Other common shrubs were *Ceanothus americanus* (New Jersey tea), *Comptonia peregrina* (sweet-fern), *Corylus americana* (hazelnut), *Prunus pumila* var. *cuneata* (sand cherry), *Rosa carolina*, *Salix humilis* (prairie willow), and *Smilax glauca* (glaucous greenbrier).

The most abundant graminoids were *Schizachyrium scoparius* (little bluestem), *Andropogon gerardii* (big bluestem), *Panicum lanuginosum* (panic grass), and *Carex pensylvanica*. Other common species were *Danthonia spicata* (wild oatgrass), *Koelaria macrantha* (June grass), and *Sorghastrum nutans* (Indian grass).

Abundant forbs were *Agalinis tenuifolia* (slender gerardia), *Aster oolentangiensis*, *Comandra umbellata* (star toadflax), *Conyza canadensis* (horseweed), *Euphorbia corollata* (flowering spurge), *Fragaria virginiana*, *Lechea leggettii* (pinweed), *Lupinus perennis* (wild lupine), *Phlox pilosa* (prairie phlox), *Potentilla simplex*, *Pteridium aquilinum*, *Rubus flagellaris*, and *Solidago nemoralis* (gray goldenrod). Other forbs included *Apocynum cannabinum* (Indian hemp), *Asclepias tuberosa* (butterflyweed), *Baptisia tinctoria* (wild indigo), *Lespedeza capitata* (bush clover), *L. hirta* (round-headed clover), *Liatris aspera* (rough blazing star), *Lithospermum canescens* (hoary puccoon), *L. caroliniense* ssp. *croceum* (hairy puccoon), *Monarda fistulosa* (wild bergamot), *Tephrosia virginiana* (goatsrue), and *Viola pedata* (birdsfoot violet).

Comments: Oak Savanna formerly covered 206 km^2 (43%) of the Oak Openings (Fig. 1). It was most abundant on sand dune ridges. Although designated as Oak Savanna on the map, many of these areas also included small patches of sand prairie on drier sites, Wet Prairie on the wetter sites, or Oak Woodland in areas more

TABLE 1

Size class distribution, relative density, and average diameter of trees in the major vegetation types of the Oak Openings of northwestern Ohio at the time of Euro-American settlement. Common names of trees are those used by the land surveyors.

Name	Diameter (cm)									Total # of Trees	Relative Density	$\bar{x}$ Diameter
	0-13	14-26	27-39	40-52	53-65	66-78	79-91	92-104	105+			
OAK WOODLAND												
White Oak (*Quercus alba*)	-	10	52	49	15	11	3	8	1	149	54.0	49.3
Black Oak (*Quercus velutina*)[1]	2	7	25	27	12	2	2	1	-	78	28.3	43.4
Elm (*Ulmus sp.*)	-	1	5	1	-	1	1	2	1	12	4.3	55.6
Hickory (*Carya* sp.)	1	3	5	1	-	1	-	-	-	11	4.0	30.2
Bur Oak (*Quercus macrocarpa*)	-	-	3	2	-	-	-	-	-	5	1.8	38.7
Oak (*Quercus* sp.)	-	-	3	-	-	-	-	-	-	3	1.1	35.6
Red Oak (*Quercus rubra*)	-	1	1	1	-	-	-	-	-	3	1.1	36.3
Red Maple (*Acer rubrum*)	-	-	1	2	-	-	-	-	-	3	1.1	39.2
Ash (*Fraxinus* sp.)	-	-	2	-	-	-	-	-	-	2	0.7	34.3
Poplar (*Populus* sp.)	1	1	-	-	-	-	-	-	-	2	0.7	19.1
Willow (*Salix* sp.)	-	1	1	-	-	-	-	-	-	2	0.7	24.5
Aspen (*Populus* sp.)	-	-	-	-	1	-	-	-	-	1	0.4	58.4
Sassafras (*Sassafras albidum*)	-	1	-	-	-	-	-	-	-	1	0.4	22.9
White Elm (*Ulmus americana*)	-	-	1	-	-	-	-	-	-	1	0.4	35.6
Sycamore (*Platanus occidentalis*)	-	-	-	-	-	-	-	-	-	1	0.4	61.0
Basswood (*Tilia americana*)	-	1	-	-	-	-	-	-	-	1	0.4	20.3
Subtotal	4	27	99	83	29	15	6	11	2	276		
OAK SAVANNA												
White Oak (*Quercus alba*)	-	14	74	102	26	9	1	4	-	230	48.5	46.0
Black Oak (*Quercus velutina*)[1]	2	21	69	61	13	5	-	2	-	173	36.5	42.2
Red Oak (*Quercus rubra*)	-	-	8	5	3	-	-	-	-	16	3.4	41.5
Bur Oak (*Quercus macrocarpa*)	-	2	7	6	-	-	1	-	-	16	3.4	38.9
Aspen (*Populus* sp.)	-	5	5	-	-	-	-	-	-	10	2.1	28.2
Elm (*Ulmus* sp.)	1	-	2	2	-	1	-	1	-	7	1.5	48.5
Black Gum (*Nyssa sylvatica*)	-	-	2	2	-	-	-	-	-	4	0.8	38.1
White Elm (*Ulmus americana*)	-	-	1	-	1	-	-	-	-	2	0.4	40.6
Basswood (*Tilia americana*)	-	-	1	1	-	-	-	-	-	2	0.4	35.6
Hickory (*Carya* sp.)	-	1	1	-	-	-	-	-	-	2	0.4	25.4
Oak (*Quercus* sp.)	-	-	-	2	-	-	-	-	-	2	0.4	48.3

TABLE 1 (*Cont.*)

Size class distribution, relative density, and average diameter of trees in the major vegetation types of the Oak Openings of northwestern Ohio at the time of Euro-American settlement. Common names of trees are those used by the land surveyors.

Name	Diameter (cm) 0-13	14-26	27-39	40-52	53-65	66-78	79-91	92-104	105+	Total # of Trees	Relative Density	$\bar{x}$ Diameter
White Ash (*Fraxinus americana*)	1	-	-	-	-	1	-	-	-	2	0.4	47.0
Poplar (*Populus* sp.)	-	1	-	-	-	-	-	-	1	2	0.4	76.2
Cherry (*Prunus serotina*)	-	-	1	-	-	-	-	-		1	0.4	35.6
Scrub Oak (*Quercus* sp.)	1	-	-	-	-	-	-	-	1	2	0.4	12.7
Willow (*Salix* sp.)	-	1	-	-	-	-	-	-	1	1	0.2	15.2
Sassafras (*Sassafras albidum*)	-	-	-	1	-	-	-	-	-	1	0.2	45.7
Red Elm (*Ulmus rubra*)	-	-	1	-	-	-	-	-	-	1	0.2	35.6
Ash (*Fraxinus* sp.)	-	-	1	-	-	-	-	-	-	1	0.2	38.1
Subtotal	5	45	173	183	43	16	2	7	1	474		
OAK BARRENS												
White oak (*Quercus alba*)[2]	-	3	10	27	1	1	-	-	-	42	57.5	43.0
Black Oak (*Quercus velutina*)[3]	-	5	4	7	5	-	-	-	-	21	28.8	31.0
Red Oak (*Quercus rubra*)	-	-	3	-	-	-	-	-	-	3	4.1	35.6
Bur Oak (*Quercus macrocarpa*)	-	-	1	2	-	-	-	-	-	3	4.1	43.2
White Elm (*Ulmus americana*)	-	-	1	1	-	-	-	-	-	2	2.7	30.5
Basswood (*Tilia americana*)	-	-	-	-	-	-	-	-	-	1	1.4	30.5
Hickory (Carya sp.)	-	1	-	-	-	-	-	-	-	1	1.4	22.9
Subtotal	0	9	20	37	6	1	-	-	-	73		
WET PRAIRIE												
White Oak (*Quercus alba*)[2]	3	7	23	24	7	1	-	-	-	65	53.7	38.7
Black Oak (*Quercus velutina*)[4]	-	5	14	11	3	1	-	-	-	34	28.1	37.6
Red Oak (*Quercus rubra*)	-	1	1	8	-	-	-	-	-	10	8.3	45.2
Aspen *(Populus* sp.)	-	6	2	-	-	-	-	-	-	8	6.6	23.5
Ash (*Fraxinus* sp.)	-	2	1	-	-	-	-	-	-	3	2.5	25.4
Basswood (*Tilia americana*)	-	-	1	-	-	-	-	-	-	1	0.8	30.5
Subtotal	3	21	42	43	10	2	-	-	-	121		

[1] <1% of these individuals are estimated to have been *Quercus coccinea* and *Q. ellipsoidalis*

[2] 3% of these individuals are estimated to have been *Quercus bicolor*

[3] >50% of these individuals are estimated to have been *Quercus palustris*

[4] >75% of these individuals are estimated to have been *Quercus palustris*

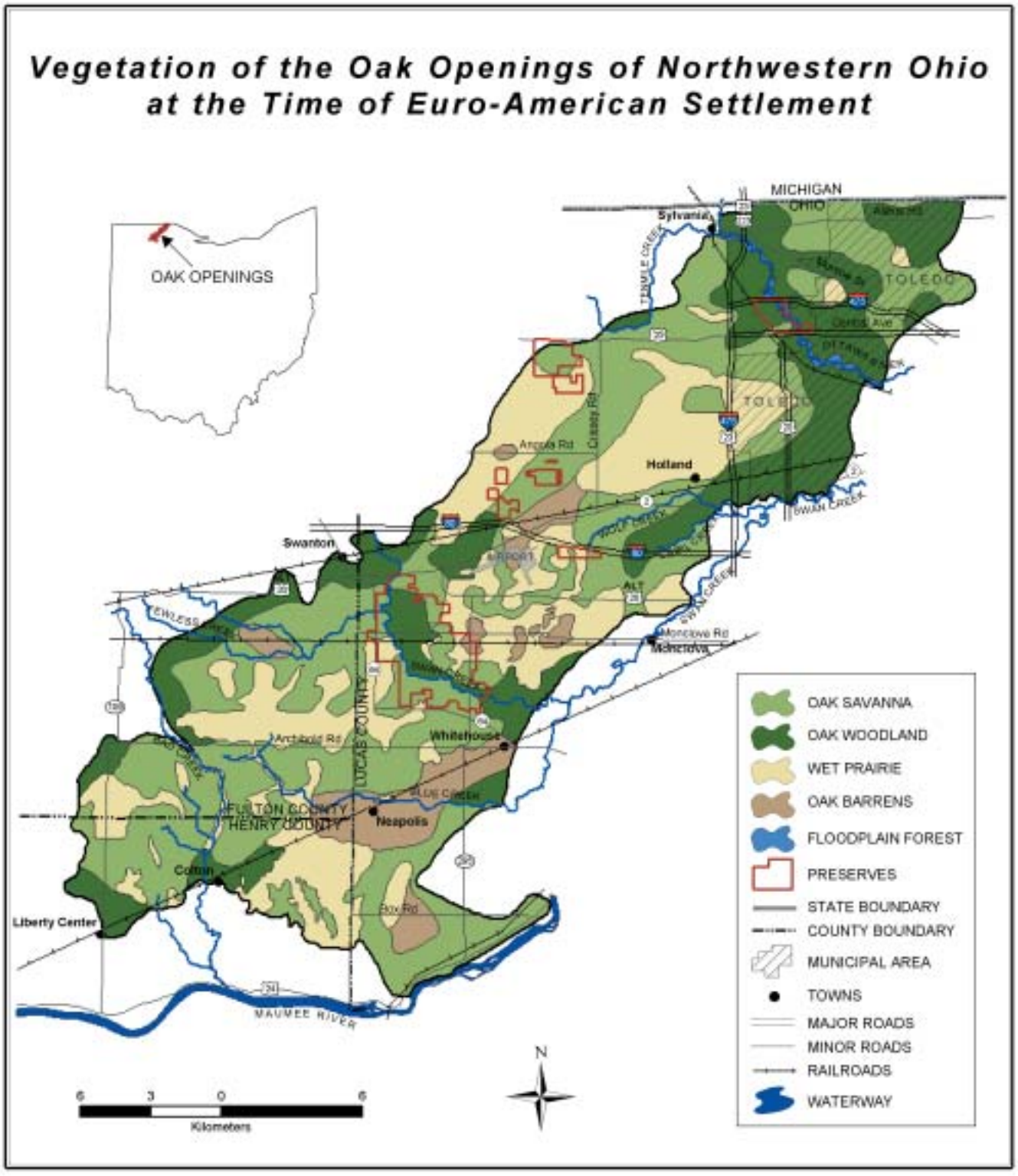

FIGURE 1. Vegetation map. (A large color version of this map [90 × 120 cm; Brewer and Vankat 2001] can be acquired through the Ohio Biological Survey, Columbus, OH.)

protected from fire.

Tree densities were less in Oak Savanna than Oak Woodland, partly because these areas were less protected from natural fires, but probably also because they were maintained by fires set by Native Americans (Gordon 1969; Huffman 1987; Dorney and Dorney 1989). Native Americans burned many areas to increase their food supply and enhance their ability to hunt wildlife. These early residents were common in the Oak Openings until perhaps the early 19th century (Hehr 1970). There are 20 records in the original land survey notes where the surveyors crossed "Indian trails," most in the southwestern portion of the Oak Openings (8 in Oak Savanna, 7 in Oak Barrens, 4 in Wet Prairie, and 1 in Oak

Woodland). At least a few Native Americans were probably still in the Oak Openings when most of the land surveys were undertaken, or they had left recently. Consequently, the influence of Native Americans on the structure and composition of the vegetation in the Oak Openings was probably still evident at that time, and thereby is represented on our vegetation map.

By the late 1800s nearly all Oak Savanna had been cleared for cropland and pasture. One uncleared area of 15 ha is in the northern part of the present Oak Openings Metropark. Although this area has changed to forest, it retains numerous large *Quercus alba* individuals, some nearly 400 years old. By the early 1900s the poor sandy soils in the northern two-thirds of the Oak Openings resulted in most agricultural areas being abandoned. Agriculture continued in many areas in the southern one-third of the Oak Openings where the soil is more fertile. Many of the areas that were abandoned in the Oak Openings reverted to Oak Savanna and, without fire, became Oak Woodland and Oak Forest. Today, there are fewer than 200 ha of Oak Savanna scattered throughout the Oak Openings (representing about 1% of the Oak Savanna present at the time of Euro-American settlement). More areas are in the process of being restored by the Toledo Metroparks through burning and other management activities (personal communication John Jaeger, Toledo Metropark Land Manager, and Scott Abella, Toledo Metropark Visiting Restoration Ecologist).

Extant Oak Savannas are different in composition from those present at Euro-American settlement. For example, *Quercus velutina* has replaced *Q. alba* as the most abundant tree. The increase of the more drought-resistant *Q. velutina* likely reflects increased soil drainage and erosion. The herbaceous layer also changed as *Lupinus perennis*, *Phlox pilosa*, and mesic grasses such as *Andropogon gerardii* declined. In contrast, xeric grasses such as *Aristida purpurascens* (arrow feather) and *Panicum capillare* (old witch grass), and weedy species such as *Poa compressa* (Canada bluegrass), *Andropogon virginicus* (broom-sedge), and *Setaria glauca* (yellow foxtail grass) increased. The most obvious difference in the shrub layer is reduced abundance of *Comptonia peregrina*.

OAK BARRENS

Composition: Oak Barrens had an average of only 2 trees/ha and was dominated by *Quercus alba*, followed by *Q. palustris* and *Q. velutina* (Table 1). Other trees included *Acer rubrum*, *Nyssa sylvatica* (black gum), *Populus tremuloides*, *Q. bicolor*, *Q. coccinea*, and *Q. palustris*. The shrubs and herbs included species found in Oak Savanna and Wet Prairie, with composition varying by topography.

Comments: Oak Barrens formerly covered 32 km^2 (7%) of the Oak Openings (Fig. 1). In general, the elevation was lower and the topography flatter than in Oak Savanna. In addition, the Oak Barrens was much wetter than the Oak Savanna or Oak Woodland, although not as wet as the Wet Prairies. After Oak Barrens dried in the summer, it probably often burned in lightning or human-set fires. Oak Barrens contained a denser layer of herbs than Oak Savanna, resulting in more intense fires. The combination of flooding and burning likely resulted in low tree density. The largest area of Oak Barrens was near the present town of Neapolis in the southern portion of the Oak Openings. Here, Moseley (1928) noted large populations of *Lupinus perennis* and *Phlox pilosa* as late as 1927, and original land surveys documented numerous *Vaccinium* bogs. The presence of these taxa and bog vegetation may be related to heavy textured soils that were more fertile than those to the north (Hehr 1970).

Today approximately three-fourths of the former Oak Barrens in the southern portion of the Oak Openings is in agriculture. Most other areas in the south were also cleared for agriculture and then abandoned. Higher elevation sites and those that were artificially drained reverted first to Oak Barrens and then to Oak Savanna, Oak Woodland, and Oak Forest. Low elevation, poorly drained sites developed into red maple and pin oak swamps. Stands of Oak Barrens in the sandier central portion of the Oak Openings were also cleared for agriculture, and approximately two-thirds were abandoned and reverted first to Oak Barrens and then to Oak Savanna and Oak Woodland on drier sites and to red maple swamps on wetter sites (the other one-third is now residential and commercial areas and old fields).

WET PRAIRIE

Composition: Wet Prairie essentially lacked trees (average density of <1 tree/ha), but the few trees present were primarily *Quercus alba*, followed by *Q. palustris* and *Q. velutina* (Table 1). Other trees included *Nyssa sylvatica*, *P. deltoides* (Eastern cottonwood), *Populus tremuloides*, and *Q. bicolor*. The dominant graminoids were *Andropogon gerardii*, *Calamagrostis canadensis* (bluejoint grass), *C. inexpansa* (bog reed grass), *Juncus canadensis* (Canada rush), *J. tenuis* (path rush), *Sorghastrum nutans*, *Equisetum arvense* (common horsetail), and *Carex scoparia* (weak stellate sedge). Other graminoids in the wetter areas included *Cladium mariscoides* (twig rush), *Typha latifolia* (common cattail), and *Scirpus validus* (soft-stem bulrush).

Common forbs included, *Asclepias incarnata* (swamp milkweed), *Epilobium coloratum* (purple-leaved willow herb), *Eupatorium perfoliatum* (bonset), *E. purpureum* (Joe-Pye weed), *Euthamia graminifolia* (grass-leaved goldenrod), *Gentiana procera* (fringed gentian), *Iris versicolor* (blue flag), *Onoclea sensibilis* (sensitive fern), *Osmunda cinnamomea* (cinnamon fern), and *O. regalis* (royal fern), *Oxypolis rigidior* (cowbane), *Polygonum pensylvanicum* (pink knot-weed), *Pycnanthemum virginianum* (mountain mint), *Rubus hispidus* (swamp dewberry), *Solidago rugosa*, *S. ulmifolia* (elm-leaved goldenrod), *Spiranthes cernua* (Ladies tresses), *Thalictrum pubescens* (tall meadow rue), *Thelypteris palustris* (marsh fern), *Verbena hastata* (blue vervain), and *Viola sagittata* (arrow violet).

The most abundant shrubs were *Cornus sericaea* (red osier dogwood), *Salix discolor* (pussy willow),

Aronia prunifolia, *Ceanothus americanus*, *Hypericum kalmianum* (Kalm's St. John's-wort), *Cephalanthus occidentalis* (buttonbush), *Sambucus canadensis* (common elder), and *Corylus americana*.

Comments: Wet Prairie formerly covered 128 km^2 (27%) of the Oak Openings (Fig. 1), primarily in low, flat areas. Sites designated as Wet Prairie by the surveyors probably also included wet mesic prairies, sedge meadows, shrub-carr, as well as small patches of bullrush marshes, cattail marshes, and a few open bogs (compare Curtis 1959; Chapman 1986). A clay layer 3-15 m below the sandy surface resulted in the accumulation of as much as 1.0 m of standing water in the winter and spring (Mayfield 1969). Much like Oak Barrens, Wet Prairie often dried in the summer and was burned by lightning or human-set fires. Wet Prairie contained a denser layer of herbs than Oak Savanna or Oak Barrens, resulting in the most intense fires in the Oak Openings. The combination of flooding and burning nearly precluded trees.

With the cessation of fires and increased drainage allowing trees to grow, many Wet Prairie areas became red maple and pin oak swamps. Other areas, especially near Toledo, have been suburbanized. The best remaining example of Wet Prairie in the Oak Openings is Irwin Prairie Preserve (Tryon 1973; Tryon and Easterly 1975). Scattered areas of Wet Prairie also are present in The Nature Conservancy's Kitty Todd Preserve and Lou Campbell State Preserve.

FLOODPLAIN FOREST

Composition: Floodplain Forest was dominated by *Ulmus americana* (American elm), *Fraxinus pennsylvanica* (green ash), *Populus deltoides*, *Salix nigra* (black willow), *Tilia americana* (basswood), and *Platanus occidentalis* (sycamore).

Comments: Floodplain Forest made up 3.0 km^2 (<1%) of the Oak Openings (Fig. 1). The only area of this vegetation described in the original land survey notes was along the Ottawa River in the northern portion of the Oak Openings. Other areas of Floodplain Forest probably occurred along Swan Creek. Today approximately one-fifth of the Floodplain Forest along the Ottawa River has been converted to residential or recreational areas, while the rest remains forest. Although much of the northern portion of this Floodplain Forest is second-growth (trees <30 cm dbh), some areas in the southern portion still have mature forests (trees 60-120 cm dbh). The composition of these forests probably changed little since Euro-American settlement. In addition to the trees mentioned above, other species in these mature forests include *Acer rubrum*, *A. saccharinum* (silver maple), *Aesculus glabra* (Ohio-buckeye), *Celtis occidentalis* (hackberry), *Gleditsia triacanthos* (honey-locust), *Quercus macrocarpa*, and *Q. rubra* (red oak). Areas of floodplain along Swan Creek presently have young forests of green ash, Eastern cottonwood, and red maple and may not represent what existed at Euro-American settlement.

VEGETATION IN THE LANDSCAPE

We determined the percentage of each major vegetation type in the Oak Openings at the time of Euro-American settlement, but it is likely that these vegetation types had been dynamic across the landscape. During long periods when high precipitation reduced fire frequencies, some stands of Wet Prairie likely increased in tree density and became Oak Barrens, some stands of Oak Barrens similarly converted to Oak Savanna, stands of Oak Savanna converted to Oak Woodland, and stands of Oak Woodland became forest. Likewise, during long periods when low precipitation increased the frequency and extent of fires and during periods of more intensive Native American land use, these vegetation trajectories were reversed. The impact of fires was likely greatest when fires followed long periods of high precipitation during which fuels accumulated.

Of the 2,716 plant species in Ohio (Cooperrider and others 2001), 1,247 (46%) have been documented in the Oak Openings (Walters 2003). With the exception of areas in southeastern Ohio (Cusick and Silberhorn 1977), the Oak Openings has the greatest species richness in the state. Despite the high plant species richness of the Oak Openings, only 21 species of trees were recorded by the surveyors in the Oak Woodland, Oak Savanna, Oak Barrens, and Wet Prairie (Table 1; the list includes 5 species that had not been differentiated by the surveyors). Moseley (1928) documented a similar number of tree species (24) in the Oak Openings in the early part of the 19th century. In contrast, the Black Swamp Forest, which surrounded the Oak Openings and had more fertile soils and much lower fire frequency, probably had 45-50 species of trees (Braun 1961; Anderson 1992).

Tree species richness for individual vegetation types was 19 for Oak Savanna, 17 for Oak Woodland, 7 for Oak Barrens, and 6 for Wet Prairie. However, direct comparison of these richness values is problematic because different numbers of trees were recorded for individual vegetation types. However, the low number of tree species in the Oak Barrens and Wet Prairie probably represents a real difference with the other vegetation types and is likely related to greater flooding and fire. This interpretation is supported by the absence of flood and fire intolerant species such as *Sassafras albidum* and *Prunus serotina* in these vegetation types.

Quercus alba was most commonly selected for bearing and line trees, with relative densities of 58% in Oak Barrens, 54% in both Oak Woodland and Wet Prairie, and 49% in Oak Savanna (Table 1). Based on Moseley's (1928) descriptions of the species in the Oak Opening and our own observations, we estimate that perhaps as much as 3% of the individuals called *Q. alba* by the surveyors in the Wet Prairie and Oak Barrens were actually *Q. bicolor*, which is primarily a wetland species. However, nearly all the individuals in the drier vegetation types (for example, Oak Woodland and Oak Savanna) were indeed *Q. alba*.

Quercus velutina was second in abundance to *Q. alba* in the four oak-dominated vegetation types: Oak Savanna (37%), Oak Barrens (29%), and both Oak Woodland and Wet Prairie (28%). However, *Quercus palustris*, a wetland species, probably made up over

50% of the individuals designated as *Quercus velutina* in Oak Barrens and over 75% in the Wet Prairie (today *Quercus palustris* is common around Irwin Prairie, one of the last remnants of Wet Prairie in the Oak Openings; Tryon and Easterly 1975). In contrast, perhaps only 1-2% of the *Q. velutina* individuals in Oak Savanna and Oak Woodland were *Q. palustris*. *Quercus coccinea* and *Q. ellipsoidalis* were also not differentiated from *Q. velutina*, but these species of dry sites were likely absent from Oak Barrens and Wet Prairie and probably accounted for less than 1% of the *Q. velutina* individuals in Oak Woodland and Oak Savanna. Therefore, *Q. velutina* had its greatest abundance in Oak Savanna, where it was able to tolerate the drier conditions. The lower abundance of *Q. velutina* in Oak Woodland may have been related to intolerance of low light levels and inability to compete with other late successional species such as *Quercus alba* (Burns and Honkala 1990). The existence of *Q. velutina* in Oak Barrens and Wet Prairie, which were wet areas before drainage following Euro-American settlement (Stone and others, 1980), is surprising given the species' preference for dry uplands (compare Burns and Honkala 1990). Individuals probably grew on small areas of raised topography within these two vegetation types and were aided by the soils becoming dry during the summer.

CONCLUSION

The vegetation map provides information on the area and distribution of the vegetation types of the Oak Openings at the time of Euro-American settlement. These data, along with new information on species composition, combine with previous studies of soils, geology, and topography to add to our understanding of the ecology of the Oak Openings. Comparison of former vegetation with present vegetation provides better understanding of past and present changes in the Oak Openings and also provides insight necessary for vegetation restoration as well as protection of rare species.

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