

The Tawawa Woods Natural Landmark:

II. Plant Species Composition and Recovery from Disturbance¹

JOHN E. SILVIUS, CADANCE A. LOWELL, AND CHRISTOPHER KNICKERBOCKER, Department of Science and Mathematics, Cedarville University, Cedarville, OH 45314 and Department of Natural Sciences and Mathematics, Central State University, PO Box 1004, Wilberforce, OH 45384-1004

ABSTRACT. Portions of Tawawa Woods, an oak-maple-beech forest community adjacent to Wilberforce (Greene Co.), OH, was granted landmark status in 1990 on the basis of its biodiversity, historic and cultural significance, and its potential as a site for studies of forest recovery from disturbance. Earlier, in 1974, Tawawa Woods was partially destroyed by a tornado that swept through nearby Xenia and vicinity. In 1988 and in 1999, we conducted studies of the plant species composition of Tawawa Woods with emphasis on tree species abundance, age, spatial distribution, and relative dominance. We used both plot sampling and point-centered quarter sampling methods. Although a total of 27 tree species were included in the samples, in 1988, 80% of the relative density was contributed by only eight species; notably, *Acer saccharum*, *Prunus serotina*, *Liriodendron tulipifera*, *Fagus grandifolia*, *Sassafras albidum*, *Fraxinus americana*, *Quercus rubra*, and *Quercus alba*. Comparisons of tree species abundance, distribution, and dominance as a function of sampling date and tree age class are discussed with regard to forest recovery from disturbance during the past 11 years, with emphasis upon the increasing importance of *Acer saccharum*. A case is made for elevating the Tawawa Woods Natural Landmark to "Natural Area" status based upon its strategic location in the Massies Creek corridor, and its ecological and historical significance.

OHIO J SCI 103 (2):12–18, 2003

INTRODUCTION

As part of an effort to identify and preserve natural areas, Tawawa Woods (Wilberforce Beech Woods), Wilberforce, OH, was included in a list of 30 "choice sites" in a report by Hunt (1956) and in an updated report by Herrick (1974). These reports, as well as one commissioned by the United States Department of Interior (Stein 1974), described the Tawawa Woods as a climax beech forest with diverse native herbaceous flora. As Stein's report was being written, Tawawa Woods incurred extensive damage from a tornado on 3 April 1974. Therefore, the report recommended that the woods be considered as a site for study of natural forest recovery from disturbance (Stein 1974).

In 1990, 22.0 ha of the Tawawa Woods were designated as the Tawawa Woods Natural Landmark in a joint agreement between the Ohio Department of Natural Resources—Division of Natural Areas and Preserves and Central State University (Merkh and Silvius 1990). In addition to its biological significance, Tawawa Woods is a testimony of past historic and cultural events that have influenced its topography and soil properties (Lowell and others 2003).

Although no quantitative ecological studies were initiated in Tawawa Woods until 1988, extensive research was being conducted on the subject of gap phase replacement (Runkle 1982; 1984). There was also a growing number of reports of the decline in recruitment of certain oak (*Quercus*) species in eastern deciduous forests (Abrams 1992; Lorimer 1993; Walters and McCarthy 1997), often in conjunction with the increasing

importance of sugar maple (*Acer saccharum*) and red maple (*Acer rubrum*) (Bonser and Aarssen 1994; Shotola and others 1992) and certain invasive exotic species such as the Asian honeysuckles (*Lonicera* sp.) (Hutchinson and VanKat 1997). Our report documents the plant species composition of Tawawa Woods with emphasis on tree species abundance, age, spatial distribution, and relative dominance at two sampling dates following the 1974 tornado; 1988 and 1999. Our results are discussed with reference to current theory of gap phase replacement following disturbance, and the effect of disturbance upon successional trends involving certain oak (*Quercus*), maple (*Acer*), and honeysuckle (*Lonicera*) species.

MATERIALS AND METHODS

Physical Environment

The Tawawa Woods Natural Landmark, Xenia Twp., Greene Co., OH (39° 43' N, 83° 52' W), is bounded by Wilberforce-Clifton Road on the west, Massies Creek on the north, and the Central State University (CSU) campus on the south and southeast (Fig. 1). Massies Creek is a major tributary of the Little Miami National Scenic River.

Tawawa Woods Natural Landmark consists of approximately 22.0 ha and includes a riparian forest at elevations ranging from 265.0 to 270.0 m.a.s.l. adjacent to Massies Creek, and an upland forest community on north-facing slopes ranging from approximately 270.0 to 300.0 m.a.s.l. near the forest edge adjacent to the CSU campus. A 5.0- to 100.0-m zone nearest the CSU campus and to the south and east of the current Landmark boundaries has a long history of more dominant human usage and disturbance (Fig. 1). This "perimeter region" is not included within the boundaries of the Tawawa Woods Natural Landmark. We have excluded it from our study because of its longer history of disturbance related

¹Manuscript received 2 April 2001 and in revised form 26 February 2002 (#01-06).

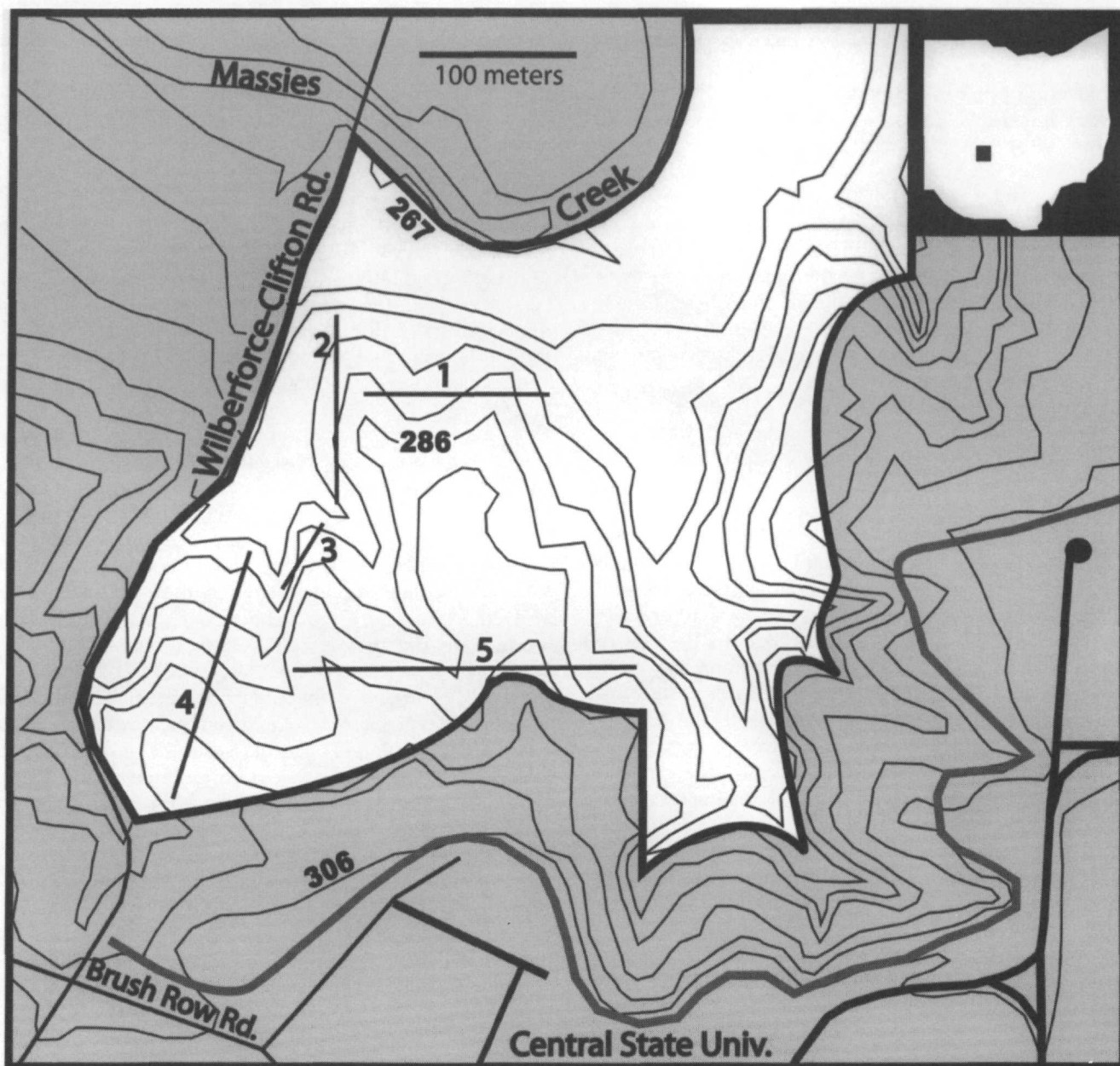


FIGURE 1. Topographic map of the Tawawa Woods Natural Landmark (unshaded area). The forest edge adjacent to the Central State University campus is delineated by the line that roughly follows the 306 m.a.s.l. contour line. The five sample transects within the Landmark are located by number. Contour interval = 4.0 m. Redrawn from the US Geological Survey 7.5-minute Xenia, OH, Quadrangle Map.

to the proximity to the forest edge.

The geologic origin of the current landscape and drainage patterns and the soil properties of Tawawa Woods are described by Lowell and others (2003). The combination of north-facing slopes, deep ravines, and frequent intermittent sharp ridges with well drained soil between ravines has produced a variety of favorable microclimates and soil substrata for a forest with high biodiversity (Lowell and others 2003). Our study focused on the forest community located on the slopes overlooking Massies Creek (excluding the "perimeter region"), hereafter referred to as Tawawa Woods.

The climate of Greene County is described as continental (Garner and others 1978); mean annual temperature for the period 1961 to 1990 was 10.9° C (NOAA

2000). Mean January and July temperatures were -2.8° C and 22.7° C, respectively. Mean annual precipitation for the period 1961 to 1990 was 100.6 cm (NOAA 2000); mean January and July precipitation amounts were reported as 5.5 cm and 10.7 cm, respectively (NOAA 2000).

Past Land Use of Tawawa Woods

With the advent of European American settlement of the Wilberforce area in the early 19th century, the management of Tawawa Woods was integrally tied to the development of Wilberforce University (Lowell and others 2003). Aerial photographs from the 1940s corroborate this claim and suggest that portions of the current forest interior were also more open and possibly used for pasturing animals (Aerial Map Archives 1948).

Sampling Methods

Tree species composition of Tawawa Woods was estimated in June/July 1988 and June/July 1999 using a combination of plot sampling and point-centered quarter sampling methods (Cottam and Curtis 1956; Brewer and McCann 1982). In 1988, a total of 41 sample points were located within Tawawa Woods by positioning line transects along major slopes in a roughly perpendicular direction to the slope, and often extending into or across ravines (Fig. 1). At random distances along each transect line, sample points were located at random distances at right angles to the left and right of the line. At each sample point, the point-centered quarter method was used to sample "medium" trees (2.5 cm to 12.9 cm diameter at breast height (DBH)) and "large" trees (DBH >13.0 cm). In addition, each sample marker served as the center point around which a 10.0 m² circle plot was positioned to sample "small trees" (at least 0.5 m tall, <2.5 cm DBH). Finally, the "tree seedling" component was sampled by counting the number of trees less than 0.5 m tall within a 1.0-m² quadrant placed within the SW quadrant adjacent to each sample point. Plot sample counts of "small trees" and "tree seedlings" are combined to estimate relative stem density of what we refer to as "small" trees. Shrubs, vines, and herbaceous flora were recorded but not included in the random sampling. Data were compiled into relative density tables and importance value tables using *TREEPLOT* software (Silvius and others 1994). Importance values were computed as the average of relative density, relative frequency, and relative dominance (based upon stem basal areas). Our sampling procedure was repeated in 1999, using the same permanently marked sample points. The Shannon Index (*H'*) (MacArthur 1955) was computed based upon the combined frequency of "medium" and "large" trees in our sampling.

In an attempt to quantify the extent of the tornado damage, we established 113.0 m² circle plots in December 2001, each centered around one of the 41 sample points. Within each plot, we recorded the number of tip-up mounds, windthrows (≥10.0 cm DBH), stumps (≥10.0 cm DBH with break ≤1.0 m above ground), "snap-offs" (≥10.0 cm DBH with break >1.0 m above ground), and damaged standing trees (≥5.0 cm DBH).

RESULTS

Tree species encountered in our sampling of Tawawa Woods totaled 27 and 28 for 1988 and 1999, respectively (Table 1). Present but not encountered in the random sampling were pawpaw (*Asimina triloba*) and sycamore (*Platanus occidentalis*), which occupied a moist alluvial area near Wilberforce-Clifton Road. Blue ash (*Fraxinus quadrangulata*) and honeylocust (*Gleditsia triacanthos*) were also present but not included in the sampling. Shrub species were represented by wild hydrangea (*Hydrangea arborescens*), common buckthorn (*Rhamnus cathartica*), bladdernut (*Staphylea trifolia*), gooseberry (*Ribes* sp.), common elder (*Sambucus canadensis*), spicebush (*Lindera benzoin*), multiflora rose (*Rosa multiflora*), and bush honeysuckle (*Lonicera maackii*).

In spite of the relatively high tree species richness in Tawawa Woods, no more than eight species combined are needed to account for 80% of the relative density in each of the size classes (Table 1). The relatively low *H'* of 1.54 for medium and large trees combined attests to the predominance of a relatively few species and low degree of evenness. For example, sugar maple (*Acer saccharum*) and black cherry (*Prunus serotina*) together represent at least 30%, and up to 85%, of the relative density in any given size-class. Among species with lower relative densities, only yellow poplar (*Liriodendron tulipifera*), American beech (*Fagus grandifolia*), and white ash (*Fraxinus americana*) attained individual relative densities over 10; these were attained in only one size-class for each species (Table 1).

In all, approximately ten more species are represented in the subcanopy and canopy layers (for example, "medium" and "large" size classes) than are recorded for the "small" size class (Table 1). This low diversity among seedlings and young saplings has been confirmed in repeated sampling experiments in Tawawa Woods by general ecology classes in 1992, 1995, 1998, and 2000 (Silvius, unpublished data). Apparently low recruitment by *Quercus* and *Carya* species (Table 1) accounts for over half of this difference.

Acer saccharum is the only prominent tree species which made major gains in importance value in both "medium" and "large" size classes. *Acer rubrum*, to a lesser extent, has increased in importance value (Table 2). On the other hand, *Liriodendron tulipifera*, *Quercus velutina*, and *Q. rubra* all have relatively high importance values and have maintained their importance in the canopy as evidenced by little or no change in importance values for "larger" trees during the 11-year period. However, all three species plus *Quercus alba* have lower importance values for "medium" trees relative to "large" trees, and demonstrate decreasing importance within "medium" between 1988 and 1999. Note that importance values for *Liriodendron tulipifera*, *Quercus velutina*, *Q. rubra*, *Q. alba*, and *Fagus grandifolia* are based heavily upon the larger average size (basal area of stems) of individual trees as reflected in the high relative dominance values. *Fagus grandifolia*, *Prunus serotina*, and *Quercus alba* each show a decrease in importance value between 1988 and 1999.

The natural diversity of microclimates and the associated flora of Tawawa Woods were significantly altered by the 1974 tornado and the subsequent clean-up. In our sampling to estimate the extent of tornado and post-tornado damage to trees present in the sample plots, tip-up mounds were found in 34% of the sample plots for an estimated density of 45.3/ha; fallen logs in 85% of plots or 312.9/ha; snap-offs in 27% of plots or 41/ha; stumps in 17% of plots or 19.4/ha. In addition, many trees, 5.0 cm DBH and larger, that were not felled directly by wind or by windthrows, sustained damage such as loss of part of the crown or a severely bent trunk and growth of lateral branches to form multiple trunks. These were encountered in 93% of plots for a density of 349.7 trees/ha.

TABLE 1

Relative density¹ of stems as a function of tree size in Tawawa Woods.

Species	1988			1999			Avg. R.D.
	Small	Medium	Large	Small	Medium	Large	
<i>Acer saccharum</i>	42.2	34.3	23.1	29.9	56.1	29.9	35.9
<i>Prunus serotina</i>	44.2	10.4	14.6	40.0	3.7	11.6	20.7
<i>Liriodendron tulipifera</i>		6.1	15.8		3.7	14.7	6.7
<i>Fagus grandifolia</i>	0.5	8.5	7.3	0.2	12.8	6.1	5.9
<i>Sassafras albidum</i>	5.2	1.2	4.9	8.2	1.2	4.3	4.2
<i>Fraxinus americana</i>	1.6	1.8	1.2	11.7	1.2	1.2	3.1
<i>Quercus rubra</i>	0.3	1.8	7.9			7.9	3.0
<i>Quercus alba</i>		0.6	7.9		0.6	4.9	2.3
<i>Carpinus caroliniana</i>	0.1	8.0	0.6	0.8	1.2		1.8
<i>Acer rubrum</i>	1.8	0.6	1.8	1.7	1.8	3.1	1.8
<i>Ostrya virginiana</i>	<0.1	3.7	2.4	0.4	3.7	1.8	2.0
<i>Ulmus rubra</i>	0.6	4.3	1.8	2.1	0.6		1.6
<i>Cornus florida</i>		5.5	1.2		1.2	1.2	1.5
<i>Ulmus americana</i>	0.1	1.8	1.2		3.7	1.8	1.4
<i>Cercis canadensis</i>		4.3			0.6	1.8	1.1
<i>Acer negundo</i>	1.4	1.2		0.6	1.2	0.6	0.9
<i>Carya</i> sp.	2.0	0.6	1.8	0.4	<0.1		0.8
<i>Acer platanoides</i>			0.6	2.1	1.2	0.6	0.8
<i>Carya cordiformis</i>		0.6		1.7	1.2	0.6	0.7
<i>Carya glabra</i>		0.6	0.6		0.6	1.8	0.6
<i>Robinia pseudoacacia</i>		0.6	1.2		<0.1	1.8	0.6
<i>Celtis occidentalis</i>		1.2		<0.1	1.8		0.5
<i>Crataegus</i> sp.		1.8			1.2		0.5
<i>Carya ovata</i>		0.6	0.6		0.6	0.6	0.4
<i>Quercus velutina</i>			1.2			1.2	0.4
<i>Quercus muehlenbergii</i>			1.2			1.2	0.4
<i>Quercus imbricaria</i>			0.6			0.6	0.2
<i>Juglans nigra</i>						0.6	0.1
Total ¹	100.0	100.0	100.0	100.0	100.0	100.0	
Species Richness ²	13.0	23.0	22.0	14.0	23.0	23.0	

¹Represents a total stem count of 1,073 in 1988, and 762 in 1999.²Number of species represented in each size class. Tree species present but not encountered in sampling are pawpaw (*Asimina triloba*), sycamore (*Platanus occidentalis*), blue ash (*Fraxinus quadrangulata*), and honeylocust (*Gleditsia triacanthos*).

DISCUSSION

Tawawa Woods is still in the midst of recovery from the effects of the 1974 tornado which affected plant populations at every level; namely, the ground level herbaceous plants, the subcanopy, and the canopy tree species. The most common disturbances at ground level resulted from treefalls and include fallen logs and

tip-up mounds. Mounds are composed largely of sub-soil brought to the surface as roots are wrenched from the ground; pits are depressions created by the displacement of soil into the adjacent mound. A sense of the degree of tornado damage to the woods can be gained by comparing the estimated density of tip-up mounds (45/ha), stumps (19/ha), and snap-offs (41/ha)

TABLE 2

Importance value and its components for dominant tree species of Tawawa Woods, 1988, 1999.

Species	Size/Year	Relative			Imp.
		Dens	Freq.	Dom.	
<i>Acer saccharum</i>	Medium				
	1988	34.3	22.9	26.8	28.0
	1999	56.1	39.6	51.1	48.9
	Large				
	1988	23.1	20.5	15.2	19.6
	1999	29.9	21.6	21.3	24.3
<i>Prunus serotina</i>	Medium				
	1988	10.4	11.4	8.4	10.1
	1999	3.7	5.5	6.9	5.4
	Large				
	1988	14.6	13.6	10.6	12.9
	1999	11.6	10.4	8.3	10.1
<i>Fagus grandifolia</i>	Medium				
	1988	8.5	7.6	28.5	14.9
	1999	12.8	14.3	10.3	12.5
	Large				
	1988	7.3	7.6	10.7	8.5
	1999	6.1	6.4	7.3	6.6
<i>Acer rubrum</i>	Medium				
	1988	0.6	1.0	0.5	0.7
	1999	1.8	3.3	1.8	2.3
	Large				
	1988	1.8	2.3	0.5	1.5
	1999	3.1	3.2	1.0	2.4
<i>Liriodendron tulipifera</i>	Medium				
	1988	6.1	6.7	6.4	6.4
	1999	3.7	4.4	5.4	4.5
	Large				
	1988	15.8	14.4	19.5	16.6
	1999	14.7	16.0	19.8	16.8
<i>Quercus velutina</i>	Medium				
	1988	0.0	0.0	0.0	0.0
	1999	0.0	0.0	0.0	0.0
	Large				
	1988	1.2	1.5	3.9	2.2
	1999	1.2	1.6	4.9	2.6
<i>Quercus rubra</i>	Medium				
	1988	1.8	2.9	2.1	2.3
	1999	0.0	0.0	0.0	0.0
	Large				
	1988	7.9	8.3	19.8	12.0
	1999	7.9	8.8	19.2	12.0
<i>Quercus alba</i>	Medium				
	1988	0.6	1.0	1.6	1.1
	1999	0.6	1.1	1.6	1.1
	Large				
	1988	7.9	8.3	8.2	8.1
	1999	4.9	5.6	5.9	5.5

to the density of standing trees of all species with DBH >60.0 cm, namely 21/ha.

The surfaces of most tip-up mounds sampled in Tawawa Woods are still largely uncolonized by plants. Plant establishment is hindered by the exposed subsoil that is low in organic matter and cation exchange capacity (Beatty 1984). Water and nutrients must not only be present but available in a balanced or congruent manner within these microsites for recolonization by herbaceous plants and tree seedlings to occur (Carlton and Bazzaz 1998). Pits adjacent to the tip-up mounds often accumulate forest litter and moisture. Thick litter accumulation in pits may physically hinder seedling establishment. Seasonal waterlogging in pits may add further to the impediment to colonization (Beatty and Sholes 1988).

In spite of the mosaic of different microsites produced on the forest floor by mounds, pits, fallen tree boles and crowns, and man-made objects that were dropped on the forest floor by the wind, Tawawa Woods has retained a diverse herbaceous flora (Lowell and others 2003). With the exception of garlic mustard (*Alliaria petiolata*) and bush honeysuckle (*Lonicera maackii*) which have invaded the perimeter of the forest and occasional treefall gaps, the herbaceous flora appears to be free of significant competition from invading species. We hypothesize that the more successful establishment of *Lonicera maackii* in the perimeter of Tawawa Woods is a result of the greater disturbance of this region by the 1974 tornado and post-tornado cleanup. Hutchinson and VanKat (1997) demonstrated that forest invasibility by *Lonicera maackii* is positively correlated with canopy disturbance, resultant high light levels, and proximity to an abundant seed source. Although the canopy of the interior of Tawawa Woods was also disrupted, the degree of disturbance and the timing of invasion of the Amur honeysuckle in this part of Greene County was such that the less disturbed forest interior could reach a point of canopy closure before the shade-intolerant shrub could establish abundant seed sources in the area.

The tree species richness of Tawawa Woods is exceptionally high with over 30 different tree species identified in the forest (Table 1). The forested Massies Creek stream corridor between Cedarville and Xenia, OH, has remained contiguous in spite of previous human intrusions and deforestation of portions of it during the era prior to 1950 (Aerial Map Archives 1948). This approximately 13.0-km corridor of continuous forest, which includes the forested slopes of Tawawa Woods, exists in sharp contrast to smaller woodlots of Greene County that are isolated within an agricultural landscape. In their survey of 17 such woodlots, Ramey-Gassert and Runkle (1992) recorded a range of 14 to 26 tree species, with an average of 20. Their comparisons of tree species composition among the woodlots demonstrated adverse effects of reduced woodlot area and increased human disturbance on species composition and richness. We think that the relatively high species richness of Tawawa Woods attests to the necessity of large, contiguous forest tracts for preservation

of plant community integrity and species richness.

No quantitative data exists for tree species composition of Tawawa Woods prior to the 1974 tornado. However, from descriptive accounts (Stein 1974) and from our sampling data, we can infer something about the forest composition prior to the 1974 tornado, and successional trends since then. According to Stein's (1974) walk-through survey of Tawawa Woods just before the 1974 tornado, the forest canopy was composed primarily of red oak (*Quercus rubra*), American beech (*Fagus grandifolia*), hickories (*Carya* sp.), and "a few sugar maples" (*Acer saccharum*). If we assume that trees in our 1988 sampling that have a DBH greater than 50.0 cm were trees large enough to have been canopy trees 14 years earlier at the time of Stein's description, the following species predominate (listed according to current relative density): *Quercus rubra* (29.4), *Liriodendron tulipifera* (23.5), *Acer saccharum* (17.5), *Quercus velutina* (11.8), *Fagus grandifolia* (11.8), and *Quercus alba* (5.9). Among canopy trees over 60.0 cm DBH, our samples included *Quercus rubra*, *Liriodendron tulipifera*, *Quercus velutina*, and *Fagus grandifolia*, suggesting a significant presence of these species extending back into the 19th century.

Gordon (1969) included most of what is now northern and central Greene County within the pre-settlement Mixed Oak Forest association. He specifically cited the Glen Helen Nature Preserve near Yellow Springs (Miami Twp., Greene Co., OH), 8.0 km N of Wilberforce, as representing a type within the Mixed Oak association, namely an Oak-Sugar Maple forest type. The Wright State University Woods, located 16.0 km W-NW of Wilberforce also has affinity to the Oak-Maple type (DeMars and Runkle 1992). Although the canopy of Tawawa Woods includes species suggestive of an Oak-Maple forest type, it also has had a significant population of *Fagus grandifolia* (hence, the name "Wilberforce Beech Woods"), normally scarce or absent from Oak-Sugar Maple associations (Gordon 1969). Gordon (1969) proposed that the persistence of *Fagus grandifolia* may be due to natural selection, "infrequent tornadoes and selective cutting of more valuable hardwoods..."

Species of the "large" size-class that occupy the canopy can be assumed to be replacing themselves if the relative densities of their respective medium and small size-classes are at least as high or higher than the relative density of their large size-classes. It follows that replacement appears likely for the principal shade-tolerant canopy species *Acer saccharum*, *Prunus serotina*, *Sassafras albidum*, and *Fraxinus americana* (Table 1). Although *Fagus grandifolia* demonstrated low recruitment of small trees for both sample years, this species is maintaining a significant role in the subcanopy ("medium" size).

That Tawawa Woods is undergoing ecological succession is supported by the fact that for both sample years we found much higher species richness and a different species composition in the subcanopy and canopy layers ("medium" and "large" trees, Table 1) than among the tree seedlings and young saplings. Based upon our data and the published literature (Lorimer

1993; Walters and McCarthy 1997), we believe the low diversity of "small" trees is due in part to the relatively high fecundity and survivorship of *Acer saccharum*, and low recruitment by *Quercus* and *Carya* species (Table 1, "small" class; Table 2).

Following the 1974 tornado, surviving subcanopy *Acer saccharum* trees quickly emerged into treefall gaps to form dense subcanopies resulting in reduced light and moisture penetration to ground level, thus limiting resource availability for competing species (Ramey-Gassert and Runkle 1992). A significant presence of *Acer saccharum* at the time of the tornado can be assumed from the high relative density of "medium" and "large" trees of this species in 1988 (Table 1). Furthermore, based upon our sampling in 1999, an estimated 10.5 individual *Acer saccharum* trees per ha were growing in an "arched-trunk" position in response to treefall damage, with two or more lateral branches having assumed vertical growth. Whereas, this distorted growth pattern enables an individual tree to participate in gap-filling as if it were multiple individuals, the eventual collapse of the supporting "arch" will inevitably reopen a canopy gap. Other species that demonstrated "arched-trunk" or multiple-trunk growth were as follows (in estimated trees per ha): *Prunus serotina* (8.4), *Cornus florida* (4.2), *Liriodendron tulipifera* (4.2), and *Acer rubrum* (2.1). Following a major forest disturbance, the presence of storm-weakened and leaning trees and those with distorted growth patterns creates a cascade of sequential events that prolongs the occurrence of gap-making and filling, and allows opportunities for a diversity of species to maintain their presence.

The success of *Acer saccharum* in gap filling has been well documented (Schneider 1966; Shotola and others 1992; Bonser and Aarssen 1994). The increase in the importance value of *Acer saccharum* among "medium" and "large" trees occurs as a result of a balanced increase in all three components of importance value; namely, relative density, relative frequency, and relative dominance (Table 2). By virtue of the way in which these "relative" values are expressed, it should be clear that an increase in the values for *Acer saccharum* means a decrease in the values for one or more other species. These changes may occur either through mortality or slower growth rates of other species, leaving the way open for *Acer saccharum* to replace the competitor species in the sample. Thus, between 1988 and 1999, 26 *Prunus serotina* trees among our sample sites were replaced by other species, as reflected in the decrease in importance values of this species (Table 2); and, 77% of these were replaced by *Acer saccharum*. Likewise, other species replaced in large part by *Acer saccharum* include *Liriodendron tulipifera* (18 trees, 50% by *A. saccharum*), *Fagus grandifolia* (9 trees, 66% by *A. saccharum*), *Carpinus caroliniana* (16 trees, 81% by *A. saccharum*), and *Quercus* sp. (13 trees, 53% by *A. saccharum*).

The increasing dominance of *Acer saccharum* in Tawawa Woods may also be attributed to possible lowering of the water table within the woods over the

past century as noted by Lowell and others (2003). Brewer (1980) suggested that the anthropogenic effect of lowering the water table in a mature climax forest in Michigan may have favored regeneration of the sugar maple. Similar anthropogenic effects in Tawawa Woods may be combining with the tornado destruction to cause numerous successional changes that justify additional periodic ecological monitoring.

In our opinion, there are several reasons why Tawawa Woods would be a significant addition to the designated Natural Areas and Preserves in Ohio. First, woody and herbaceous plant diversity appears to be equal to or greater than several long-standing forest preserves in SW Ohio. Second, the presence of *Fagus grandifolia* distinguishes Tawawa Woods from the more typical Oak-Sugar Maple forest preserves in the area, and from Hueston Woods, a Beech-Maple forest near Oxford, OH. Third, its potential as a site to study forest regeneration after disturbance and its historic significance in the development of European and African American culture in the Wilberforce area have been demonstrated in this article and its companion (Lowell and others 2003). Finally, the location of Tawawa Woods along Massies Creek, a major tributary to the Little Miami National Scenic River, makes it of strategic value in the protection of aquatic and terrestrial biodiversity in southwestern Ohio.

ACKNOWLEDGMENTS. This research was completed in part with a grant from the Ohio Biological Survey and financial support from Cedarville University and Central State University. The authors also wish to acknowledge Larry Cox and Alvadell Silvius for their valuable assistance in the field studies, data analysis, and archival research. We appreciate the valuable expertise from Dara Fraley in developing Figure 1.

LITERATURE CITED

- Abrams MD. 1992. Fire and the development of oak forests. *BioScience* 42(5):346-53.
- Aerial Map Archives. 1948. Soil Conservation Service and Greene County Cooperative Extension Service, Xenia, OH.
- Beatty SW. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology* 65:1406-19.
- Beatty SW, Sholes ODV. 1988. Leaf litter effects on plant species composition of deciduous forest treefall pits. *Can J For Res* 18:553-9.
- Bonser SP, Aarssen LW. 1994. Plastic allometry in young sugar maple (*Acer saccharum*): adaptive responses to light availability. *Am J Bot* 81(4):400-6.
- Brewer R. 1980. A half-century of changes in the herb layer of a climax deciduous forest in Michigan. *J Ecol* 68:823-32.
- Brewer R, McCann MT. 1982. *Laboratory and Field Methods in Ecology*. Philadelphia (PA): Saunders College Publ.
- Carlton GC, Bazzaz FA. 1998. Resource congruence and forest regeneration following an experimental hurricane blowdown. *Ecology* 79(4):1305-19.
- Cottam G, Curtis JT. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37:451-60.
- DeMars BG, Runkle JR. 1992. Groundlayer vegetation ordination and site-factor analysis of the Wright State University Woods (Greene County, Ohio). *Ohio J Sci* 92(4):98-106.
- Garner DE, Ritchie A, Siegenthaler VL. 1978. Soil Survey of Greene County, OH. US Dept. of Agric. Soil Conservation Service. 105 p.
- Gordon RB. 1969. The natural vegetation of Ohio in pioneer days. *Bull Ohio Biol Surv, New Series* 3(2). 109 p.
- Herrick JA. 1974. The natural areas project: a summary of data to date. Ohio Biological Survey Informative Circular #1. Columbus, OH. 60 p.
- Hunt KW. 1956. A preliminary survey of the Ohio natural areas. Mimeograph, "restricted, not for publication." Washington (DC): The Nature Conservancy. 7 p.
- Hutchinson TF, VanKat JL. 1997. Invasibility and effects of Amur honeysuckle in southwestern Ohio forests. *Conserv Biol* 11(5):1117-24.
- Lorimer CG. 1993. Causes of the oak regeneration problem. In: Loftis DL, McGee CE, editors. *Oak Regeneration: Serious Problems, Practical Recommendations*. Asheville (NC): USDA, Forest Service, Gen Tech Rep SE-84. p 14-39.
- Lowell CA, Silvius JE, Darrow S. 2003. The Tawawa Woods Natural Landmark: I. Survey of flora and land use history. *Ohio J Sci* 103(2):2-11.
- MacArthur RH. 1955. Fluctuations of animal populations, and a measure of community stability. *Ecology* 36:533-6.
- Merkh NA, Silvius JE. 1990. Preserving ecological diversity in southwest Ohio: the importance of Wilberforce Beech Woods. 8th Annual Central State University Science Symposium, Wilberforce, OH.
- NOAA. 2000. Midwestern Regional Climate Center. Champaign, IL. <http://mcc.sws.uiuc.edu/Summary/Data/339361.txt>
- Ramey-Gassert LK, Runkle JR. 1992. Effect of land use practices on composition of woodlot vegetation in Greene County, Ohio. *Ohio J Sci* 92(1):25-32.
- Runkle JR. 1982. Patterns of disturbance in some old-growth mesic forests of Eastern North America. *Ecology* 63:1533-46.
- Runkle JR. 1984. Development of woody vegetation in treefall gaps in a beech-sugar maple forest. *Holarctic Ecology* 7:157-64.
- Schneider G. 1966. A twenty-year investigation in a sugar maple-beech stand in southern Michigan. *Res Bull #15*. 61 p.
- Shotola SJ, Weaver GT, Robertson PA, Ashby WC. 1992. Sugar maple invasion of an old-growth oak-hickory forest in southwestern Illinois. *Amer Midl Nat* 127(1):125-38.
- Silvius JE, Sjoquist DW, Mundy DD. 1994. Vegetation analysis using a computer spreadsheet. *Am Biol Teach* 56(1):41-3.
- Stein CB. 1974. Evaluation of Tawawa Natural Area (Wilberforce Beech Woods), Ohio, as a National Natural Landmark. David H. Stansbery, Project Supervisor. The Ohio State University Museum of Zoology, Columbus, OH, for US Dept of the Interior National Park Service, Contract Order 590L20387.
- Walters GM, McCarthy BC. 1997. Forest decline and tree mortality in a southeastern Ohio Oak-Hickory forest. *Ohio J Sci* 97(1):5-9.