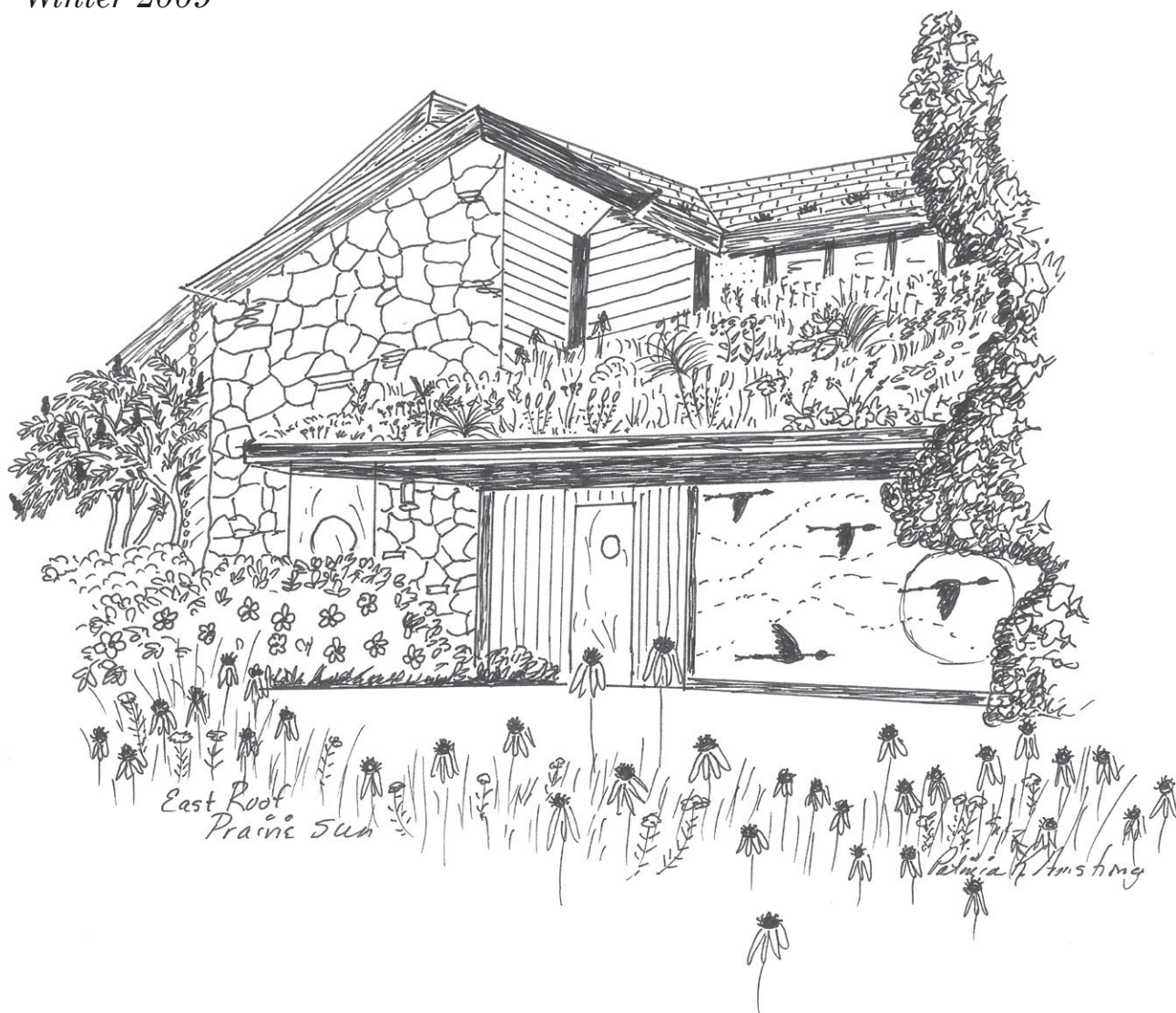


ERIGENIA

Number 22
Winter 2009



Journal of the
Illinois Native Plant Society

ERIGENIA

Number 22, Winter 2009

The Illinois Native Plant Society Journal

The Illinois Native Plant Society is dedicated to the preservation, conservation,
and study of the native plants and vegetation of Illinois.

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Illinois Native Plant Society
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e-mail: ilnps@aol.com

ERIGENIA is named for *Erigenia bulbosa* (Michx.) Nutt. (harbinger of spring), one of our earliest blooming woodland plants. The first issue was published in August, 1982.

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COVER ILLUSTRATION: Drawing by Patricia Armstrong of the green roof on the Armstrong residence, study area of this feature article.

Greetings.

Welcome back to ERIGENIA. I am very grateful for the opportunity to serve as editor of the journal and excited by this challenge. Hiking in the parks, preserves and other areas of natural beauty all over the state is my favorite pastime and I look forward to learning more about the plants of Illinois.

There has been a hiatus of several years in publishing the journal. Rather than try to catch up with multiple issues, we have decided to get back on schedule with a fall publication date. This can only be accomplished with your help. Please submit original research for the next issue before June, 2009.

In this issue, we have incorporated abstracts of research projects funded by the Society. It is exciting to see where our research dollars go. In many cases these are the future botanists of Illinois, the caretakers of our native flora.

Please do not hesitate to send me a note with your ideas for essays or inquiries about research possibilities. The journal is yours and is not possible without your contributions.

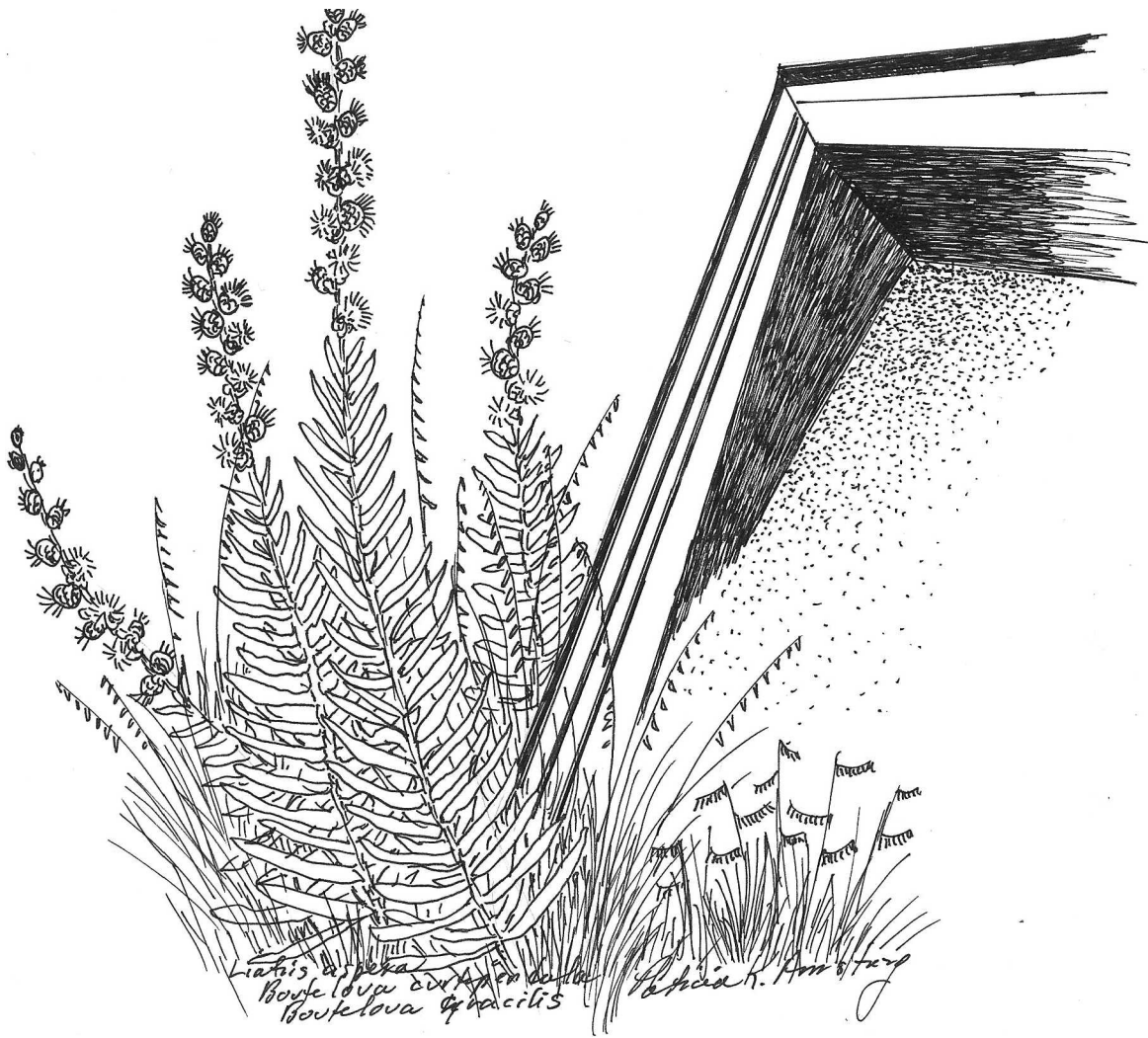
Tracy Evans, Editor

ERIGENIA

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Salix aspera
Bouteloua curtipendula
Bouteloua gracilis
L. H. R. Armstrong

ABOUT OUR AUTHORS

Patricia K. Armstrong has a B.A. in Biology from North Central College in Naperville and an M.S. in Botany-Ecology from the University of Chicago. She has been a traditional and non-traditional educator for many years. She managed the Schulenburg Prairie. She now runs a private consulting business, Prairie Sun Consultants, from her passive solar electric home in Naperville.

W. Clark Ashby taught forest ecology and other botany courses at the University of Chicago and later Southern Illinois University at Carbondale from the 1940s to 1992 when he retired. He is a Past President of the Southern Chapter of the Illinois Native Plant Society.

Victoria A. Borowicz has a B.S. from UW-Green Bay and a M.S. and Ph.D. from Penn State. She holds a research (adjunct) appointment at Illinois State University where she studies the impact of mycorrhizal fungi on host plant-insect herbivore relations and the role of a hemiparasite in a prairie community.

Daniel T. Busemeyer is currently an Environmental Planner with Ghostpine Environmental Services Ltd. in Calgary, Alberta. His primary duties include writing environmental conservation and reclamation reports for pipelines, wellsites and access roads and ensuring legislative compliance with regard to various environmental issues relating to oil and natural gas development. He earned an M.S. in Biological Sciences from the University of Cincinnati and a B.S. in Anthropology from the University of Chicago.

Ann Claerbout is a botanist and wetland scientist with HDR Alaska in Anchorage, AK. She received her M.S. in botany from the University of Illinois, where her research focused on endangered plants of the Midwest and the use of native plants in landscaping. Her most recent experience is with botanical surveys in Alaska including invasive species inventories, range assessments, and botanical inventories in Southcentral, Interior, and Western Alaska.

Janice M. Coons is a botany professor at Eastern Illinois University and is active in the Illinois State Academy of Science and the Botanical Society of America. She teaches classes including plant physiology and horticulture. Her research involves reproductive biology of rare prairie species with restoration applications as well as propagation of native species for use in landscaping.

Kari Foster Cretini is currently an ecologist with the U.S. Geological Survey at the Coastal Restoration Field Station of the National Wetlands Research Center in Baton Rouge, LA. She received her M.S. in Plant Biology from Southern Illinois University in 2004.

Bob Edgin is a field representative for the Illinois Nature Preserves Commission. His research focuses on the structure and composition of forest and prairie communities and population dynamics of endangered plant species within Illinois nature preserves.

John Ebinger is emeritus professor of botany at Eastern Illinois University. His research focuses on the structure and composition of forest, glade and sand prairie communities in Illinois as well as the tropical genus *Acacia*.

James Ellis works as a field botanist and plant ecologist for the Critical Trends Assessment Program at the Illinois Natural History Survey. His interests include conservation, protection and restoration of prairie and other natural areas throughout central Illinois.

Paul Z. Gulezian is a Ph.D. candidate in ecology and evolutionary biology at the University of Illinois at Chicago (UIC). His research interests include analyzing ecological patterns and processes relating to the success of invasive plant species in the midwestern United States. Paul is also a fellow in the NSF-funded LEAP (Landscape, Ecological and Anthropogenic Processes) program at UIC that endeavors to train Ph.D. students in an interdisciplinary approach to the study of urban ecosystems.

ABOUT OUR AUTHORS, continued

Peter Jackson is a life scientist with the U.S. Environmental Protection Agency in Chicago, where he works on water quality standards and monitoring issues. He is also steward at Deer Grove Forest Preserve in Cook County. In 2005 Mr. Jackson completed a vegetation study of Middlefork Savanna in Lake County as part of his Master's thesis, and this study is presented herein.

Alicia Mullarkey is currently working as a Plant Ecologist Intern with the Missouri Department of Conservation. She is also graduate student in the Biology Department at Illinois State University studying the effects of inbreeding and interpopulation outcrossing on garlic mustard populations.

William E. McClain is an adjunct research associate in botany at the Illinois State Museum in Springfield, Illinois. His interests include forest and prairie ecology, exotic species, and rare plants.

Beth Middleton is a Research Ecologist with the National Wetlands Research Center of the U.S. Geological Survey in Lafayette, Louisiana. Her studies look at the role of climate change in the function and distribution of worldwide wetlands. Her Ph.D. is from Iowa State University, and was on the role of goose grazing in monsoonal wetlands in India.

Dennis Nyberg is on the faculty of the Department of Biological Sciences. He is also the Director of the James Woodworth Prairie, owned by the University of Illinois at Chicago.

Henry R. Owen is a botany professor at Eastern Illinois University. He teaches wide range of courses for majors, non-majors and M.S. students. His research areas include plant physiology, genetics, and tissue culture.

Loy R. Phillippe is the collections manager for the vascular plants and fungi at the Illinois Natural History Survey. His primary duties include herbarium computerization, specimen collection and preparation and the daily operations of the herbarium. Loy earned a B.S. and M.S. in botany from Eastern Illinois University and a Ph.D. in plant taxonomy from the University of Tennessee.

Matthew Richardson is a doctoral candidate in the Program in Ecology, Evolution, and Conservation Biology at the University of Illinois Urbana-Champaign and research mechanisms that influence patterns of biodiversity.

Sedonia Sipes is an associate professor in the Plant Biology Department at Southern Illinois University Carbondale. Research in her lab focuses on the evolutionary ecology of pollination relationships, particularly those involving native specialist bees.

Brent Todd worked with the Threatened and Endangered Plant Species Research Program at Eastern Illinois University in Charleston as both an undergraduate and graduate biology student and later as an instructor. He is currently director of the Dual Credit Program at Lake Land College in Mattoon, Illinois.

FEASIBILITY OF USING PRAIRIE VEGETATION ON A SLOPED ROOF WITH FOUR INCHES OF SOIL

Patricia K. Armstrong¹

ABSTRACT: Growing prairie on roofs has become more common in the last few years and usually involves a flat roof with a foot or more of soil. This paper explores the possibility of growing prairie plants on a 30 degree sloped roof in four inches (10 cm) of soil where only *Sedums* have proved successful. Three thousand plugs, seedlings and dormant root plants were planted on a roof in Naperville, IL, in May of 2005. The palette consisted of 75 species (90% of which were native to the Midwest and sandy-droughty areas near by). Twelve species of *Sedum*, including 4 native, were included to improve probability of success. Due to extreme drought conditions, delicate seedlings were watered the first growing season. Over 90% of the 3000 plants survived the summer. Three species failed to come up. Seven species (8%) had some difficulty. Fifty-one species (65%) bloomed the first year. Almost all of the plants survived the first winter. The study will continue over the next few years to evaluate which species can not only survive the extreme conditions on the roof but hopefully reproduce and thrive.

INTRODUCTION

Green roofs (roofs with grass or other vegetation planted on them) have been around since ancient times. Early pioneers in U.S.A. frequently used prairie sod for building blocks as well as roofs for their homes on the prairie where there were no trees for building materials. In modern times many European countries (over 35 years in Germany) as well as the United States have begun to use vegetated green roofs as a means of lowering temperatures in cities where there are vast areas of concrete and asphalt. Green roofs also hold and cleanse rainwater and therefore help in storm water management and flood control. They add to the insulation value of the building, and they can be attractive and useful areas for people to relax and enjoy nature or to plant vegetable gardens. Most green roofs are flat and on tops of large business or industrial buildings with at least a foot (30.5 cm) of soil. Prairie vegetation and even small trees and shrubs have worked very well under these circumstances.

The purpose of this study is to test if prairie vegetation can be used on a sloped roof with a mere 4 inches (10 cm) of soil. Most green roof specialists recommend using only non-native *Sedums* under these conditions. Prairie Sun Consultants, Naperville,

Illinois, and Foliage Design Systems, Lombard, Illinois, designed a study to determine the feasibility of using prairie plants on a sloped roof with only 4 inches (10 cm) of soil. The study occurred at a private single family dwelling in southwest DuPage County ~30 miles west of Chicago in 2005–2006.

MATERIALS AND METHODS

Study site

The home is a passive solar, energy-efficient home designed and built by the author and her husband in 1983. The original cedar wood shake roof was in need of repair so a new roof was planned and installed the fall of 2004.

Methods

The new roof consisted of three different parts: (1) photo voltaic solar-electric panels on top of the upper dormer covered with 30# half-lap rolled roofing; (2) interlocking aluminum shingles made from recycled beer and soda pop cans installed on the shaded north and west parts of the roof and the smaller ridges and sides of the dormer; and (3) the 4 inch (10 cm) soil green roof over the two largest areas of the roof which have a 6:12 pitch (roughly 30 degrees). These areas included the east-facing roof measuring approximately 500 square feet (46.5 square meters) with partial shading by the upper part of the house to the south

¹ Prairie Sun Consultants, 612 Staunton Road, Naperville, Illinois 60565.

and west and overhanging trees to the north. It gets full sun in the morning and early afternoon and is shaded by late afternoon. The south facing roof over the largest part of the house is approximately 1000 square feet (93 square meters) in size with full sun exposure throughout the day.

Since the lot is completely landscaped with over 300 species of native plants (most of which are prairies species) construction could not begin until fall when the plants went dormant. Therefore the old shingles were removed and the new shingles, waterproofing layers, cribbing and soil were installed in October and November of 2004. Because the home was passive solar with 6 inch (15 cm) walls and 12 inch (30.5 cm) rafters, no further strengthening of the roof was required. Nevertheless, a special light-weight soil mix was used so to not exceed 25 pounds/square foot (102.24 kilos/square meter) weight.

Two layers of thick polyglass waterproofing membrane were heat sealed on the roof. Then a slope-stabilization system of wood and plastic cribbing was installed to help hold the soil in place. The next layers consisted of a thick plastic root barrier, a geonet B sheet drain, an Enka mat open net for soil stabilization and drainage, and finally the 4 inches (10 cm) of soil. The roof was topped off with a heavy erosion blanket in November 2004.

The winter 2004–2005 was spent researching plant species to use, locating suppliers and ordering all the plants. Approximately 150 species were considered most of which were native to the prairies of the upper Midwest. Plants were selected for their short height, tolerance of temperature extremes, wind and drought, and therefore primarily included species of sandy and well drained habitats, or soil-less rocky glades. Because of the generally held view that only *Sedums* would work in such shallow soil, an assortment of 12 *Sedums* were selected of which 4 were native to Illinois and the U.S.

Seventy five species were located and ordered from 10 different nurseries. The design consisted of sweeping bands of plants taking into consideration their responses to sun, shade, wind, and drought. Plants were combined and blended with companion species. The final design utilized 3000 plants, 90% of which were native. Most of the plants were 2 to 4 inch (5 to 10 cm) plugs, some were dormant roots, and some were tiny, delicate seedlings. The roofs were divided into sections according to the 2 × 4 cribbing so there were 22 sections on the east roof with 9 to 48 plants in a section (most had 32) and 26 sections on the south roof with 28 to 84 plants in a section (most had 72). It took 3 days to assemble all the plants, 4 days to sort them out and package them for the individual sections of the roof, and 4 full days to plant all 3000 plants. Initial planting was finished on May 20 2005. By June

12, 2005, all back ordered plants had been added to the roof requiring another full day of planting.

The 2005 growing season was the driest in the recorded history of northern Illinois. No significant rain fell for nearly 4 months. Total rainfall for the year was 10 inches (25.4 cm) below normal therefore we watered the roof to help the plants grow (especially the tiny seedlings).

Maintenance

First year growing season:

- (1) The roof was watered every day the first week and every week until September;
- (2) The roof was weeded; several weeds came in with the transplants, some flew in on their own (Table 2); and
- (3) In November, the tall plants were cut and the cuttings left as mulch all winter.

Second year growing season:

- (4) In March 2006 most of the dead vegetation was cut off and cuttings swept off the roof;
- (5) It was noted which plants did not survive the winter (cold and snow problems); and
- (6) Some plants that did poorly were replaced with the same species. These included:
 - a. *Coryphantha vivipara* was mostly dug out by animals, only 8 survived;
 - b. *Psoralea esculenta*, *Anemone canadensis*, *Anemone carolina*, *Sisyrinchium campestre*, never came up, dormant roots were replaced by the supplier (free of charge);
 - c. *Sedum pulchellum* and *Talinum calycina*, annuals, needed more seeds;
 - d. *Carex pensylvanica*, tiny seedlings died and were replaced;
- (7) Some plants that died were replaced with other species:
 - a. *Lewisia cotyledon* and *Sempervivella alba* were replaced with *Coryphantha vivipara*;
 - b. *Tradescantia virginiana* was replaced with *Tradescantia ohioense* and *Lupinus perennis*;
- (8) *Artemisia ludoviciana* was removed because it was too aggressive and spreading;
- (9) Some new species were added: *Lupinus perennis*, *Callirhoe involucrata*, *Tradescantia ohioense*, and *Viola striata*;
- (10) Only new plants were watered.

Spring 2006 was very exciting with many new species blooming: *Anemone patens*, *Geum triflorum*,

Phlox bifida, *Phlox pilosa*, *Antennaria rosea*, and *Penstemon caespitosus*. Observations will continue throughout the rest of this, the second, growing season and in succeeding years as well.

RESULTS

Plants that were planted on the roof spring 2005 are listed in Table 1. Items shown include the origin of each species, how they were planted, when they were planted, and when they first bloomed. Weeds found growing on the study site in 2005 and 2006 are listed in Table 2. Items shown include the name of each weed and possible sources for the weed. Over 90% of the plants survived their first growing season and first winter. Four species (5%) did not come up or were not seen the first growing season. Ten species (13%) had some difficulty or did not grow well their first growing season. Fifty species (67%) bloomed their first growing season. Plants on the roof bloom weeks before the same species blooms on the ground, and plants on the roof also finish blooming and go dormant before the same species on the ground. Very few plants were lost from March to July of the second growing season (2006). Most plants which were too young to bloom in 2005 bloomed in 2006.

CONCLUSIONS

The green roof in this study is currently in the middle of its second growing season and thus some conclusions are not final. So far most of the plants are doing well. Less than 10% of the species have failed to survive. All plants are increasing in size and about 50% of the soil is now covered with plants. Most of the plants are much taller than expected, and some of them are having difficulty keeping their tall stems upright without thick support from other plants and some flowers are lying down. Multitudes of seedlings are appearing in the spaces between plants which means that the original landscape design of sweeping bands of colors and textures will become somewhat blurred in the future. In

the 2007 season only new plants were watered so some drought effect on plant survival was expected.

LITERATURE CITED

- Bower, J. 2003. The tallest tallgrass prairie. Audubon. National Audubon Society. September:18 pp.
- Chicago Department of Environment. No date. A guide to rooftop gardening..
- Dunnett, N. and N. Kingsbury. 2004. Planting green roofs and living walls. Portland, Oregon: Timber Press. 254 pp.
- Fedun, I. 2003. Tennessee Ecoroof: Newsletter of North American Native Plant Society. Fall:8-9.
- Holtcamp, W. 2001. A grass-roofs effort. Sierra May-June:24-27.
- Kleine, A. 2001. Rooftop garden cools Windy City. The American Gardener. July-August:59 pp.
- Miller, C. 2002. Updating the sod roof. Landscape Architecture. November:30 pp.
- Miller, M. 2006. Not a sprinkler in sight. Chicagoland Gardening. January-February:48-53.
- Phalen, T. 1999. Updated rooftops. pp. 10-15 in The American Gardener.
- Snodgrass, E. C. and L. L. Snodgrass. 2006. Green roof plants: A resource and planting guide. Portland, Oregon: Timber Press. 204 pp.
- Ulrich, C. 2001. Sky high roof gardening in Chicago. Chicagoland Gardening. March-April:51-57.
- Wisby, G. 2005. Home's green roof has a slant to it. Illinois Solar Energy Association Heliographs. June:7 pp.

For Further Reading

- Armstrong, C. and P. Armstrong. 2006. A Roof over Their Heads, Native Plants, Spring, 6 pp.
- Bonnin, J. 2006. Raising the Roof, Native Plants give green roofs a Sustainable Twist, Wildflower, 23:1, Fall 2006, pp. 12-19.
- Peltier, P. No date. Taking Landscape to New Heights, the Landscape Contractor, pp. 20-22.

Table 1: List of plants that were planted on the roof of the house at 612 Staunton Road in Naperville, Illinois, 2005 and 2006. Items shown include the origin of each plant, how they were planted, when they were planted, when they first bloomed, and how each species fared.

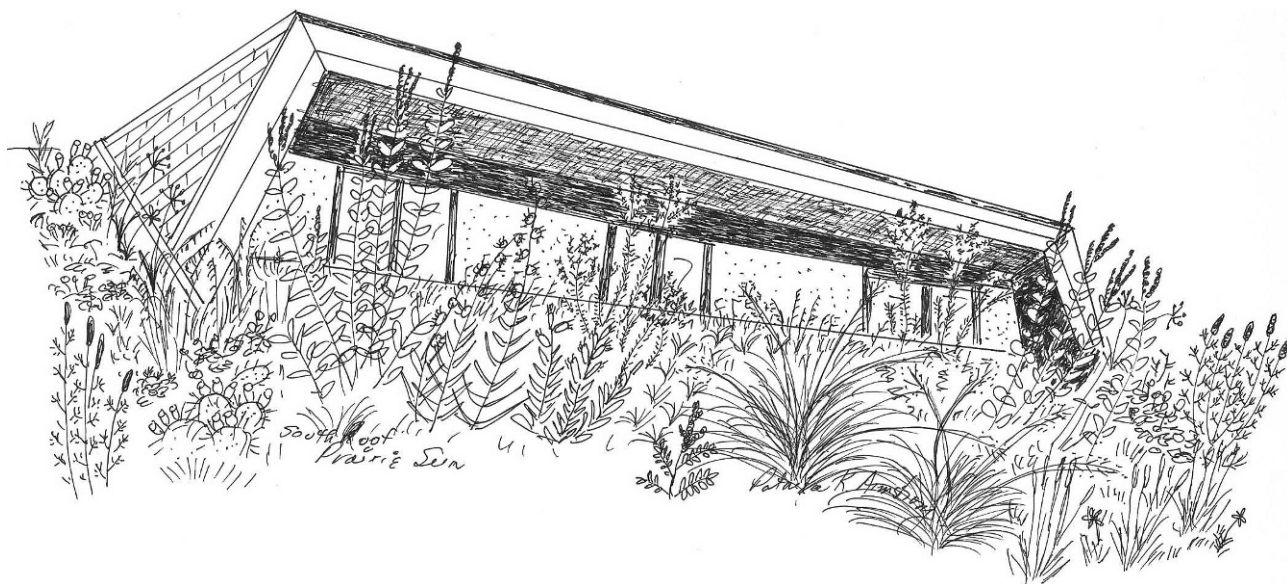
Species	Origin	Plant type	Planted	Bloomed	Status
<i>Achillea millefolium</i>	Europe	2-4" plug	May 2005	2005	Did very well
<i>Allium stellatum</i>	prairie	dor. root	May 2005	2005	Did very well
<i>Amorpha canescens</i>	prairie	seedling	May 2005	Jun 2006	Grew well
<i>Andropogon scoparius</i>	prairie	2-4" plug	May 2005	Sep 2005	Did very well
<i>Anemone canadensis</i>	prairie	dor. root	May 2005		No plants 2005, replanted 2006
<i>Anemone carolina</i>	prairie	dor.root	May 2005		No plants, replanted 2006
<i>Anemone patens wolfgangiana</i>	prairie	2-4" plug	May 2005	Mar 2006	Did very well
<i>Antennaria rosea</i>	G.plains	2-4" plug	May 2005	May 2006	Did very well
<i>Aquilegia canadensis</i>	woods	2-4" plug	May 2005	Jun 2005	Did very well
<i>Artemisia ludoviciana</i>	G.plains	seedling	May 2005	Sep 2005	Too aggressive, too tall, pulled most of it 2006
<i>Asclepias tuberosa</i>	prairie	seedling	May 2005	Jun 2006	Grew very well
<i>Asclepias verticillata</i>	prairie	seedling	May 2005	July 2006	Grew very well
<i>Aster ericoides</i>	prairie	2-4" plug	May 2005	Aug 2005	Grew very well
<i>Aster laevis</i>	prairie	volunteer	May 2005	Sep 2005	Grew very well
<i>Aster macrophyllus</i>	woods	dor. root	May 2005	Aug 2006	Grew very well
<i>Aster novae-angliae</i>	prairie	volunteer	May 2005	Sep 2005	Grew very well
<i>Aster sericeus</i>	prairie	2-4" plug	May 2005	Sep 2005	Did very well
<i>Blephilia ciliata</i>	prairie	2-4" plug	May 2005	Jul 2005	Did very well
<i>Bouteloua curtipendula</i>	prairie	volunteer	May 2005	Jul 2005	Did very well
<i>Bouteloua gracilis</i>	G.plains	plug/seed	May 2005	Jul 2005	Did very well
<i>Bouteloua hirsuta</i>	G.plains	seedling	May 2005	Jun 2006	Did well
<i>Buchloe dactyloides</i>	G.plains	2-4" plug	May 2005	Jul 2005	Did very well
<i>Callirhoe involucreta</i>	G.plains	large p.	May 2006	Jun 2006	Died
<i>Callirhoe triangulata</i>	prairie	seedling	May 2006	Jul 2006	Grew well
<i>Carex bicknellii</i>	prairie	2-4" plug	May 2005	Jun 2005	Did very well
<i>Carex pennsylvanica</i>	savanna	seedling	May 2005		Died, replanted 2006
<i>Carex pennsylvanica</i>	savanna	2-4" plug	May 2005	June 2005	Did very well
<i>Carex rosea</i>	woods	2-4" plug	May 2005	June 2005	Did very well
<i>Chrysopsis camporum</i>	prairie	large p.	May 2006	May 2006	Died
<i>Coreopsis grandiflora</i>	G.plains	2-4" plug	May 2005	Jun 2005	Lost some winter 05-06
<i>Corydalis aurea</i>	G.plains	2-4" plug	May 2005	Jun 2005	Did very well
<i>Coryphantha vivipara</i>	G.plains	2-4" plug	May 2005		Squirrels dug up, 8 survived to 2006, replanted 2006
<i>Echinacea angustifolia</i>	G.plains	2-4" plug	May 2005	Jun 2005	Did well
<i>Echinacea pallida</i>	prairie	2-4" plug	May 2005	Jun 2005	Did well
<i>Eragrostis spectabilis</i>	prairie	2-4" plug	May 2005	Sep 2005	Did very well
<i>Erigeron annuus</i>	prairie	volunteer	May 2005	May 2006	Did well
<i>Euphorbia corollata</i>	prairie	seedling	May 2005	Jul 2006	Grew well
<i>Gaillardia pulchella</i>	G.plains	2-4" plug	May 2005	Jul 2005	Lost some winter 05-06
<i>Geum triflorum</i>	prairie	2-4" plug	May 2005	Jun 2005	Did very well
<i>Heuchera richardsonii</i>	prairie	2-4" plug	Jun 2005	May 2006	Did well
<i>Hymenoxys grandiflora</i>	Rockies	2-4" plug	May 2005		Grew slowly, dwindled 2006
<i>Koeleria cristata</i>	prairie	2-4" plug	May 2005	Jun 2006	Did well
<i>Lewisia cotyledon</i>	G.plains	2-4" plug	May 2005	Jun 2005	None survived winter 2005/6 winter, did not replace
<i>Liatis aspera</i>	prairie	2-4" plug	May 2005	Sep 2005	Did well
<i>Liatis cylindracea</i>	prairie	2-4" plug	May 2005	Sep 2005	Did well
<i>Liatis punctata</i>	G.plains	dor.root	May 2005	Aug 2006	Did well

Table 1: Continued

Species	Origin	Plant type	Planted	Bloomed	Status
<i>Linum perenne lewisii</i>	G.P. Eur	2-4" plug	May 2005	May 2006	Did very well
<i>Lupinus perennis</i>	prairie	large p.	May 2006	May 2006	Died back,
<i>Monarda punctata</i>	prairie	seedling	May 2006	May 2006	Grew well
<i>Oenothera missouriensis</i>	G.plains	2-4" plug	May 2005	Jun 2005	Did very well
<i>Opuntia humifusa</i>	prairie	2-4" plug	May 2005	Jun 2005	Did very well
<i>Penstemon caespitosus</i>	G.plains	2-4" plug	May 2005	Jun 2005	Did very well
<i>Penstemon hirsutus</i>	prairie	2-4" plug	May 2005	May 2006	Did very well
<i>Petalostemum purpureum</i>	prairie	seedling	May 2005	Jun 2006	Grew well
<i>Phlox bifida</i>	prairie	2-4" plug	May 2005	Apr 2006	Did very well
<i>Phlox pilosa</i>	prairie	2-4" plug	May 2005	Jun 2005	Did very well
<i>Polemonium reptans</i>	woods	2-4" plug	May 2005	May 2006	Did very well
<i>Psoralea esculenta</i>	G.plains	dor.root	May 2005		Dissappeared early, added a few more 2006
<i>Ratibida columnifera</i>	G.plains	2-4" plug	May 2005	Jun 2005	Not very many in 2006
<i>Rudbeckia speciosa</i>	prairie	2-4" plug	May 2005	Jun 2005	Lost some winter 05-06
<i>Sedum acre</i>	Eurasia	2-4" plug	May 2005	Jun 2005	Grew slowly
<i>Sedum album</i>	Eurasia	seedling	May 2005	Jun 2006	Grew slowly
<i>Sedum floriferum</i>	Russia	2-4" plug	May 2005	Jun 2006	Did well
<i>Sedum kamtschaticum</i>	Russia	2-4" plug	May 2005	Jul 2005	Did well
<i>Sedum lanceolatum</i>	G.plains	seedling	May 2005		Grew slowly
<i>Sedum pulchellum</i>	glades	2-4" plug	May 2005	May 2005	Annual, planted again 2006
<i>Sedum spectabile 'neon'</i>	Eurasia	2-4" plug	May 2005	Aug 2005	Did well
<i>Sedum spurium 'Fuldaglut'</i>	Eurasia	seedling	May 2005	Jun 2006	Did well
<i>Sedum spurium 'Dragonblood'</i>	Eurasia	2-4" plug	May 2005	Jun 2006	Did well
<i>Sedum stenopetalum</i>	G.plains	seedling	May 2005		Grew slowly
<i>Sedum tatarowinii</i>	Asia	2-4" plug	May 2005	Jul 2005	Did well
<i>Sedum ternatum</i>	woods	2-4" plug	May 2005	May 2006	Did very well
<i>Sempervivella alba</i>	Asia	2-4" plug	May 2005		None survived winter 2005/6, did not replant
<i>Sisyrinchium campestre</i>	prairie	dor.root	May 2005	May 2006	Did not see in 2005, replanted 2006
<i>Solidago nemoralis</i>	prairie	2-4" plug	May 2005	Sep 2005	Did well
<i>Solidago sciaphila</i>	cliffs	large p.	May 2005	Sep 2005	Did well
<i>Solidago speciosa</i>	prairie	2-4" plug	May 2005	Sep 2005	Did well
<i>Sporobolus heterolepis</i>	prairie	2-4" plug	May 2005	Sep 2005	Did well
<i>Talinum calycina</i>	S.E.	seedling	May 2005	Jul 2005	Did well
<i>Talinum rugospermum</i>	sand	volunteer	May 2005	Jul 2005	Came back 2006
<i>Tradescantia ohioense</i>	prairie	small p.	May 2006		Transplanted from vegetable garden
<i>Tradescantia virginiana</i>	prairie	2-4" plug	May 2005	Jun 2005	Lost most winter 2005/6, did not replace
<i>Verbena stricta</i>	prairie	2-4" plug	May 2005	Aug 2005	Did very well
<i>Viola papilionacea/sororia</i>	woods	dor. root	May 2005		Added small plants from yard 2006
<i>Viola pedata lineariloba</i>	prairie	dor.root	May 2005	May 2006	Didn't see in 2005, replanted 2006
<i>Viola striata</i>	woods	small p.	May 2005	May 2006	Added small plant from yard 2006

Table 2: List of weeds found growing on the roof of the house at 612 Staunton Road in Naperville, Illinois, 2005 to 2006.

Species	Probable source
<i>Acer saccharinum</i>	seeds helicopter in from tree across the street
<i>Artemesia ludoviciana</i>	in original planting but too tall and aggressive so decided to remove
<i>Cardamine hirsuta</i>	seeds in transplants?
<i>Celtis occidentalis</i>	seeds brought in by birds or squirrels?
<i>Chaenorrhinum minus</i>	showed up 2006, seeds in transplants? I have no idea on this one
<i>Digitaria sanguinalis</i>	was not weeded out of transplants when planted
<i>Erigeron canadensis</i>	showed up 2006, seeds in transplants?
<i>Euphorbia supina</i>	showed up 2006, seeds in transplants?
<i>Lactuca serriola</i>	seeds fly in from weedy parkway
<i>Oenothera biennis</i>	seed carried to roof by birds or squirrels?
<i>Oxalis stricta</i>	was not weeded out of transplants when planted
<i>Panicum capillare</i>	showed up 2006, probably was in transplants
<i>Senecio vulgaris</i>	was not weeded out of transplants when planted
<i>Sonchus aspera</i>	showed up 2006, seeds in transplants?
<i>Taraxacum officianale</i>	was not weeded out of transplants when planted
<i>Ulmus americana</i>	seeds blew in from parkway tree
<i>Veronica arvensis</i>	seeds in transplants?



TEMPORAL AND SPATIAL VEGETATION DYNAMICS IN A REMNANT OAK SAVANNA: MIDDLEFORK SAVANNA, LAKE COUNTY, ILLINOIS

Peter W. Jackson¹

ABSTRACT: Oak savanna was a dominant ecosystem in the upper Midwest, but was almost completely destroyed after European settlement. In 2005 I conducted a study of a rare high-quality, remnant silt-loam savanna located at Middlefork Savanna in Lake County Illinois. I documented the vegetation structure, composition and diversity of the savanna, assessed changes in these parameters since 1996 under a regime of active management, and assessed how the distribution and richness of ground layer species were associated with light availability and soil conditions.

There was a statistically significant structural change (Chi-square goodness-of-fit test) in the overstory, associated with a shift in the distribution of trees from larger to smaller size classes, mostly due to the recruitment of a large number of small *Carya ovata* (Mill.) K.Koch (shagbark hickory) saplings. Total shrub layer stem density declined significantly (Wilcoxon signed ranks test) from 12,460 stems/ha in 1996 to 1,400 stems/ha in 2005. The ratio of non-native to native shrub stems also decreased significantly (Chi-square test) from 1.3 in 1996 to 0.1 in 2005. The ground layer of the savanna at Middlefork was unusually species-rich, with a count of 163 species in 50 1 m² plots. Forbs were dominant, comprising 108 taxa and 41.5% of total plot cover across all 50 plots. A significant (paired samples t-test) increase in mean plot species richness (from 15.4 to 17.3) and two diversity indices (Shannon and Simpson) indicated that management is restoring the site in a manner consistent with management goals for the site.

Detrended correspondence analysis of the ground layer vegetation indicated that percent open canopy was the most highly-correlated environmental factor with the distribution of plots in species space. Nearly as important were magnesium, calcium, cation exchange capacity, percent moisture, photosynthetically-active radiation, pH, and percent organic matter. Direct gradient analysis indicated that half of the species were centrally-oriented along the light gradient, supporting the hypothesis that there is a characteristic savanna flora, with a number of species that may exhibit peak abundance in savannas. Medians for the remaining species fell in either the sunniest or the most shaded deciles, confirming the importance of a wide range of light availability in promoting diversity in the savanna ground layer. Canonical correspondence analysis results confirmed the collective importance of several environmental factors on the distribution of plant species in the ground layer.

INTRODUCTION

Prior to European settlement, much of the Midwestern U.S., including significant portions of north-eastern Illinois, was covered by oak savanna (Curtis 1959; Kilburn 1959; Nuzzo 1986; Leach and Ross 1995). Savannas are communities of sparse trees and shrubs dominated by a continuous herbaceous ground layer (Curtis 1959; Leach and Ross 1995). Oak savanna lies on a vegetative continuum between prairie and forest, and is thought to have been maintained in

an open mosaic of patchy microhabitats of light and shade primarily by fire, interacting with topography and other factors (Curtis 1959; Anderson 1983; Pruka 1994; Leach 1996; Taft 1997). Although the dominant plants in a savanna are those making up the ground layer, natural community classification systems generally distinguish savannas from other communities in terms of their percent canopy cover. Most contemporary studies have adopted the 10–50% canopy cover range to define savannas (Pruka 1994; Bowles and McBride 1996; CRBC 1999).

Unfortunately, oak savannas in the upper Midwest have been almost completely destroyed since settlement (Curtis 1959; Nuzzo 1986; Pruka 1994; Leach 1996; Bowles and McBride 1996). Nuzzo (1986)

¹ U.S. Environmental Protection Agency, 77 W. Jackson Blvd. Chicago, Illinois 60604.

estimated that a mere 0.02 percent of the original 11–13 million hectares of Midwestern oak savanna remains as relatively high-quality savanna. Most remnant savannas are severely degraded, largely due to fire suppression; in the absence of fire, oak savannas have succeeded into closed forests. Overgrazing, conversion to agricultural use, fragmentation and timber harvesting have also contributed to the decline of oak savannas (Leach and Ross 1995). Given the historic extent of these ecosystems in the Chicago region, and the vast destruction of these communities since settlement, restoration of oak savanna remnants, has been identified as a high priority for biodiversity conservation in the region (CRBC 1999).

As a result of the loss and degradation of savannas that has occurred, there is little good information about the presettlement structure, composition, and dynamics of oak savanna plant communities, particularly with respect to understory vegetation (Pruka 1994; Leach and Ross 1995; Bowles and McBride 1996). Thus, meaningful restoration of degraded savanna remnants is hampered by the lack of high-quality remnant savanna sites that can serve as references for restoration (Bowles and McBride 1996). Concepts about what these systems were like and suggested guidelines for how they should be restored have thus proven to be quite controversial (Packard 1988, 1993; Anderson 1991; Mendelson et al. 1992; Pruka 1994; Leach and Givnish 1999).

Savannas have been characterized as being high in species diversity relative to prairies and woodlands (Pruka 1994; Leach and Givnish 1999), but as yet few studies have thoroughly examined relationships between the distribution of species and spatial variation in light levels, soil characteristics, seed dispersal, fire coverage patterns, etc. Such correlations could help to identify mechanisms that may be responsible for high spatial species turnover and other vegetative patterns, and help refine management priorities for the restoration of oak savannas in the region.

The main objectives of this research were to: 1) document the structure, composition and diversity of the plant community of Middlefork Savanna, a remnant, mesic silt-loam savanna located in Lake County, Illinois; 2) assess changes in the structure, composition and diversity of the savanna plant community that have occurred since 1996; and 3) assess the extent to which the distribution and richness of savanna ground layer species are associated with a variety of environmental factors, including light availability and soil conditions.

I addressed two groups of research hypotheses, those related to temporal trends and those related to spatial patterns. For temporal trends, the general research hypothesis was that restoration actions are

meeting the goals identified in the management plan for the site (Lake County Forest Preserve District undated), which include removal of invasive species and re-introduction of native species. I made and evaluated the following testable predictions: Between 1996 and 2005, the savanna in Unit One should have experienced a significant: 1) decrease in *Rhamnus cathartica* L. (common buckthorn) small (< 5 cm dbh) shrub stem density; 2) decrease in *Lonicera tatarica* L. (Tartarian honeysuckle) small (< 5 cm dbh) shrub stem density; 3) decrease in non-native and total shrub stem densities (< 5 cm dbh); 4) decrease in the ratio of non-native to native small (< 5 cm dbh) shrub stem density; 5) decrease in tree sapling (< 5 cm dbh) stem density; 6) decrease in abundance of lower size class (up to 35 cm) trees and large shrubs (≥ 5 cm dbh); 7) increase in ground layer native species richness; and 8) effective control (no significant increase) of populations of non-native invasive herbaceous species present onsite, including *Alliaria petiolata* (M. Bieb.) Cavara & Grande (garlic mustard), *Lythrum salicaria* L. (purple loosestrife), *Phalaris arundinacea* L. (reed canary grass), and *Dipsacus laciniatus* L. (cut-leaved teasel).

For the assessment of spatial patterns, the general research hypotheses were that plant species distributions are associated with various environmental factors. I made and evaluated the following predictions related to the spatial distributions of species: The distributions of ground layer species should exhibit significant correlations with: 1) light availability; 2) soil moisture; 3) soil texture; 4) soil temperature; 5) soil nutrients (P, K, Ca, Mg, total %N); 6) soil pH; and 7) soil percent organic matter.

METHODS

Site description

Middlefork Savanna, located near Lake Forest in Lake County, Illinois (Figure 1), is a large complex of more than 182 hectares of oak savanna, prairie, woodland, wetland, and agricultural land in nine management units (Figure 2). The focus of this study is an 11.7-hectare, high-quality oak savanna contained within Management Unit One (Figure 3). This mesic silt-loam savanna is considered by some to be one of only two remaining high-quality remnant oak savannas on fine-textured soil in northeastern Illinois (Bowles et al. 2004), and is one of the very few high-quality savannas of this type in the entire Midwest (Nuzzo 1986). The savanna is representative of the “oak openings” savanna type as described by Curtis (1959), which is characterized by groves of large, open-grown bur oaks, with a canopy cover of up to 50% and an abundance of herbaceous species, both graminoids

and forbs, comprising the ground layer. The site is located within the Northeastern Morainal Natural Division of Illinois (Schwegman 1973), and the soils are primarily clay, clay loam, and loam glacial till. According to Bowles et al. (2004), the site has persisted due to light grazing and fires ignited historically from the railroad running along the western boundary. Dominant trees on the site are *Quercus macrocarpa* Michx. (bur oak), *Q. alba* L. (white oak), and *Q. ellipsoidalis* E. J. Hill (Hill's oak) (Bowles et al. 2004). The site was officially designated as an Illinois Nature Preserve on September 5, 2002 (K. Neal, pers. comm.).

The vegetation at Middlefork was surveyed in 1986 and again in 1996 (Bowles et al. 2004). The site lost native species richness during the interval and was becoming overrun with *Rhannus cathartica* and other invasive species. Since 1996 the site has been intensively managed for removal of invasive species (Ken Klick, pers. comm.). This course of events presented a unique opportunity to assess vegetative changes at the site in light of management actions undertaken since 1996.

Data Collection

I used the sampling methodologies of Bowles et al. (2004) to sample the plant community. The four permanently marked, randomly-placed east-west transects (100 m, 180 m, 60 m, and 160 m) of Bowles et al. (2004) were relocated and marked with flags at each 10 m point, which were used as center points for ground layer plots.

Ground layer vegetation was sampled between June 16–26, 2005. I defined ground layer vegetation as all herbaceous plants, plus all woody plants < 1.0 m in height. I sampled ground layer vegetation in 50 1 m² (1 m × 1 m) plots established at 10-meter intervals along each transect beginning at ten meters. Within each plot, I recorded cover class for the total coverage of each major growth form (forbs, graminoids, and woody plants), and presence and cover class of each species of ground layer plant rooted within the plot. I recorded percent cover using the same cover classes as the 1996 study: <15%, 15–30%, 31–50%, 51–70%, 71–90%, and > 90%. As an additional measure of plant species abundance in the ground layer, the 1 m² sampling frame was divided with string into one hundred 10 cm × 10 cm squares; I then recorded the number of these smaller square decimeters (dm²) occupied by rooted plants of each species (Bowles et al. 2004). Nomenclature followed Swink and Wilhelm (1994) with one exception: I refer to one species of oak as Hill's oak (*Quercus ellipsoidalis*) rather than scarlet oak (*Q. coccinea* Münchh.) to be consistent with the previous study of the site.

Canopy trees and the shrub layer were sampled on August 14 and 20, 2005. I recorded to species all trees ≥ 5 cm diameter at breast height (“dbh”, where breast height is 1.4 m above the ground) in ten 100 m² plots (2 m × 50 m) centered on each transect. I recorded trees in four diameter size classes: 5–15, >15–35, >35–55, and >55 cm; for trees > 55 cm, the exact dbh was also recorded. Small trees and shrubs (< 5 cm dbh but ≥ 1 m tall) were recorded to species in ten 50 m² plots (1 m × 50 m), on the left side of the transect and thus nested within the wider tree plots.

Two measures of light availability were recorded at each ground layer plot. On July 31, 2005 under mostly clear skies I measured percent canopy openness, defined as the proportion of sky hemisphere not obscured by vegetation (Jennings et al. 1999), using digital hemispherical images taken with a FC-E8 Nikon Fisheye Converter lens (180° field of view) mounted on a Nikon Coolpix 950 digital camera. Images were taken within three hours of sunset to avoid overexposure and maximize contrast between canopy vegetation and sky. The camera was mounted one meter above the center of each plot on a tripod with the lens axis vertical, the image plane leveled, and the top of the camera oriented toward magnetic north. All canopy photos were analyzed on a PC using the Gap Light Analyzer (GLA) image analysis software (Frazer et al. 1999).

On August 28, 2005 I directly measured solar radiation at each plot between 11 a.m. and 2 p.m. under clear skies using a Licor LI-250 Light Meter (Licor, Inc., Lincoln, NE). Instantaneous photosynthetically-active radiation (PAR) was measured in μmol s⁻¹ m⁻² by placing the sensor one meter above each plot. A fifteen-second average was recorded by selecting the “AVG” setting on the sensor and moving it around above the 1 m² plot in a systematic manner. I also measured solar radiation under full sunlight in an open field outside of the savanna, immediately prior to and after the recording of PAR measurements; the highest reading was used to rescale each PAR reading as a percent of full sun.

I also measured several soil characteristics. On June 2, 2005 I used a 1.9 cm diameter soil corer to obtain for each 1 m² quadrat a 15 cm soil core sample from immediately outside each quadrat corner. These four soil cores were combined. The resulting 50 composite samples were used to determine percent soil moisture gravimetrically (Brower et al. 1998), and the samples were then shipped to A&L Laboratories (Memphis, TN) for analysis of nutrients, cation exchange capacity, texture, percent organic matter and pH. Soil moisture and temperature were also measured periodically with electronic probes.

DATA ANALYSIS

Correlations

To measure the association between (dm^2) frequency counts and percent cover midpoints, I conducted Spearman rank correlation analyses by species, by plot, and by diversity index. A Bonferroni adjustment was made to the critical value to maintain an experiment-wide critical value of $\alpha = 0.05$, and the resulting individual test critical value was 0.008. I also conducted a Spearman rank correlation between percent canopy openness, as measured using digital hemispherical photos, and percent PAR, as measured with the light meter.

Characterization of Savanna Vegetation, 2005

Using my data from 2005, I calculated importance values (Brower et al. 1998) for each tree species as the average of its relative density and relative basal area (calculated using midpoints of diameter classes) per hectare. For small trees and shrub species I calculated density per hectare. For ground layer species I calculated at the site level: species diversity using the exponential Shannon index and the inverse of Simpson's index, species evenness using Shannon's and Simpson's evenness indices, and actual and jackknifed species richness (Krebs 1999). In addition, I calculated for the site the floristic quality index (FQI), a standardized method for assigning a qualitative measure of habitat quality to a plant community in the Chicago region (Swink and Wilhelm 1994). At the plot level I calculated: mean plot total richness, mean plot native richness, and mean plot non-native richness. For each ground layer species I calculated mean plot cover and plot frequency. For ground layer growth forms (forbs, graminoids, and woody plants), I calculated mean plot cover based on overall plot coverages. I used these various calculations and indices to document the structure, composition and diversity of the plant community. All diversity indices were calculated in Microsoft Excel 2002 (Microsoft Inc, Redmond WA).

Temporal Change in Savanna Vegetation (1996–2005)

To assess structural change in the tree community between 1996 and 2005, I compared the frequency distribution of stem densities across size classes using the Chi-square goodness-of-fit test and the 1996 size class distribution as the "expected" values. For shrubs and small trees, I was not able to normalize the data, so I tested for significant differences in plot densities using the nonparametric Wilcoxon signed ranks test. For the ground layer, all data sets were evaluated for normal distributions and homogeneity of variances. Where one of these conditions was lacking, I attempted to normalize the data using several transformation functions. Based

on the outcome of the transformations, I used either a paired t-test or the Wilcoxon signed ranks test to test for significant differences in: a) diversity, evenness, and overall species richness for the site; b) native, non-native, and total plot species richness; and c) mean plot cover and frequency of selected individual species. I used Microsoft Excel 2002 to conduct the Chi-square test, and I used SPSS Version 12.0 (SPSS Inc, Chicago, IL) to run all statistical tests. I also calculated the percent similarity (Krebs 1999) of the 50 ground layer plots between 1996 and 2005.

Spatial Patterns in Savanna Ground Layer

I conducted an ordination analysis of ground layer plots using PC-ORD Version 4 (McCune and Mefford 1999). I initially conducted correspondence analysis (also called reciprocal averaging). As the correspondence analysis indicated the presence of an arch effect and compressed axis ends, I ran a detrended correspondence analysis (DCA), which corrects for these problems when they occur (McCune and Mefford 1999).

I also conducted a direct gradient analysis using plot frequency data to characterize ground layer species distributions over the light gradient. Following a methodology employed by Pruksa (1994) in a study of an oak savanna in Wisconsin, I first ranked the 50 plots in descending order according to the percent canopy openness above them. Next, I divided the 50 plots evenly into ten groups of five plots ("deciles") based on their relative percent canopy openness rankings. Thus, the five sunniest plots were grouped together, followed by the five next sunniest plots, and so on. For each species, the frequencies for each group of plots were then summed to derive a total of ten frequency totals (one per decile). Species were then ranked according to their relative positions along the light gradient based on the decile which contained their median frequency values.

Again using PC-ORD Version 4 (McCune and Mefford 1999), I conducted a canonical correspondence analysis (CCA) to assess the strength of the relationship between the distribution of plant species in the ground layer and seven environmental factors that had the highest r^2 values in correlation analyses with the DCA scores. The seven environmental factors were: percent open canopy, magnesium, calcium, cation exchange capacity, percent moisture, PAR as a percent of full sun, and pH.

RESULTS

Correlation of Ground Layer Abundance Measures

Table 1 summarizes the results of the Spearman rank correlation analyses of the two methods used to

sample ground layer vegetation abundance (percent cover and dm² frequency). The results indicate that a highly significant positive correlation exists between these alternative methods (Bonferroni-adjusted significance level of 0.008; r_s from 0.429 to 0.860; d.f. = 49; p from < 0.001 to 0.002).

Correlation of Canopy Openness and Solar Radiation

Canopy openness ranged from 17–65% across the 50 plots with a mean of 29%. In contrast, PAR as a percentage of full sun ranged from 3–100% across the plots with a mean of 31%. Again, the Spearman correlation was significant ($r_s = 0.65$; d.f. = 49; $p < 0.001$), indicating a strong and very highly-significant correlation between canopy openness and PAR across the site.

Characterization of Savanna Vegetation, 2005

Based on importance values, Hill's oak (*Quercus ellipsoidalis*) was dominant, accounting for one-third (33.9%) of the total stand importance values (Table 2). The high importance of *Q. ellipsoidalis* is due to both its large basal area (1st in rank) and its high density (2nd in rank). Shagbark hickory (*Carya ovata*) was second in importance with a value of 23.6%; this high score is primarily due to the large number of small *C. ovata* saplings in the savanna. In addition to the large number of *C. ovata* saplings, I recorded six small (5–15 cm dbh) *Q. ellipsoidalis* and three small *Q. macrocarpa*, indicating that some recruitment is occurring for these species (Table 2). The largest tree recorded in 2005 was a 75 cm dbh *Q. macrocarpa*.

Total tree density in the Unit One savanna was 450/ha (Table 2; Figure 5). Of these, 62% (280/ha) was in the smallest size class (5–15 cm dbh), 31% (140/ha) was in the 15–35 cm size class, no trees were recorded in the 35–55 cm size class, and only 7% (30 trees/ha) was in the largest size class (> 55 cm dbh).

Shrubs and tree saplings averaged 1400 stems/ha; 1180 (84.3%) were shrubs, and 220 (15.7%) were saplings. The most abundant shrub was *Corylus americana* Walter (American hazelnut) at 640 stems/ha (94% in one plot), followed by *Cornus racemosa* Lam. (gray dogwood) at 220 stems/ha and *Spiraea alba* Du Roi (meadowsweet) at 120 stems/ha (found in one plot; Table 3). Exotic shrub species were relatively sparse, comprising only 120 stems/ha, or 8.6% of total shrub layer stem density. The ratio of non-native to native shrub stems was 0.135.

The ground layer of the Unit One savanna at Middlefork contained a total of 163 species, 140 native and 23 non-native. First-order jackknifed species richness was 209, and the floristic quality index for the site was 53.2. Mean total richness within plots was 17.3 species, and mean native plot richness of was 14.3

species. All richness, diversity and evenness indices for the site are presented in Table 4.

Mean plot cover and plot frequency for all recorded ground layer species are presented in order of abundance in Appendix 1. Despite the striking diversity in the ground layer at Middlefork, five of the top ten species in mean plot cover were invasive species.

Among growth forms in the ground layer, forbs were dominant, comprising 108 species (66.2% of all species encountered) and 41.5% of the total mean plot cover across all 50 plots (Table 4). Graminoids (grasses, sedges and rushes) were second in abundance with 37 species (22.7% of all species) and 25.6% mean plot cover, and woody plants were least abundant, with 18 species (11.0% of all species) and 14.4% mean plot cover.

Temporal Change in Savanna Vegetation, 1996–2005

Chi-square goodness-of-fit test results indicated that there was a statistically significant change in the structure of the tree community between 1996 and 2005 in the Middlefork Unit One savanna (Chi-square = 9.41; d.f. = 3; $p < 0.025$). The key structural change was a relative shift in the distribution of trees from the larger size classes to the smallest size class (Figures 4 and 5), largely due to the recruitment of a large number of small shagbark hickory saplings (Table 5).

From 1996 to 2005, the total shrub layer stem density declined dramatically at Middlefork from 12,460 stems/ha to 1,400 stems/ha (Table 6). Wilcoxon signed ranks test results indicated that this decrease in stem density was statistically significant for shrubs ($Z = -2.497$; d.f. = 9; $p = 0.013$), which declined from 11,420 to 1,180 stems/ha, but not for saplings ($Z = -1.761$; d.f. = 9; $p = 0.078$) even though the density of saplings declined from 1,000 to 220 stems/ha (Table 6). The ratio of non-native to native shrub stems also decreased significantly from 1.3 in 1996 to 0.1 in 2005 (Chi-square = 46; d.f. = 1; $p < 0.001$), confirming that the decrease in stem density was far greater for non-native shrubs than for native shrubs.

Among individual shrub species, by far the most dramatic change was the significant reduction ($Z = -2.934$; d.f. = 9; $p = 0.003$) in *Rhamnus cathartica* stem density from 5680 to 60 stems/ha, a decline of approximately 99%. Another non-native shrub, *Lonicera tatarica* was reduced by more than 90% from 640 to 60 stems/ha, a change that was marginally significant ($Z = -1.863$; $p = 0.063$). Among native shrubs, *Cornus racemosa* was significantly reduced by 94% from 3720 to 220 stems/ha ($Z = -2.313$; $p = 0.021$).

Mean species richness within ground layer plots increased significantly from 15.4 to 17.3 species

between 1996 and 2005 ($t = -2.080$; d.f. = 49; $p = 0.043$). Mean native plot richness increased significantly from 13.2 to 14.2 ($Z = -6.096$; $p < 0.001$), and mean non-native plot richness also increased significantly from 2.2 to 3.0 ($t = -2.416$; $p = 0.019$). Likewise, both the exponential Shannon diversity index and the inverse Simpson diversity index increased significantly (from 13.71 to 15.87 [$t = -2.246$; $p = 0.029$] and from 12.09 to 14.30 [$t = -2.147$; $p = 0.037$], respectively). Neither evenness index changed significantly between 1996 and 2005 (Shannon changed from 0.95 to 0.96 [$Z = -.983$; $p = 0.325$], and Simpson changed from 0.79 to 0.81 [$Z = -.601$, $p = 0.548$]). All 1996 and 2005 richness, diversity and evenness indices for the site are presented in Table 4.

In the ground layer of the Unit One savanna, I also detected some dramatic shifts in the abundance of individual species. For example, the mean plot cover of *Helianthus divaricatus* L. (woodland sunflower) increased from 3.3 to 5.6% (marginally significant: $Z = -1.882$, d.f. = 49, $p = 0.060$), and mean plot cover of *Corylus americana* increased from 0.6 to 2.0% (non-significant: $Z = -1.382$; $p = 0.167$) between 1996 and 2005.

Two non-native, invasive species of concern in the Middlefork Unit One savanna due to their well-known propensity to increase rapidly are *Alliaria petiolata* and *Phalaris arundinacea*. However, *A. petiolata* was present in only two plots in both years, and declined in mean plot cover from 0.6 to 0.3% from 1996 to 2005 (not significant: $Z = -0.552$; d.f. = 49; $p = 0.581$). The frequency of reed canary grass, however, increased from three to nine plots, and mean plot cover increased significantly from 0.45 to 3.21% ($Z = -2.047$; $p = 0.041$). Another invasive species, the native *Solidago altissima* L. (tall goldenrod), increased significantly from 3.2 to 6.6% ($Z = -2.918$, $p = 0.004$), and was the most abundant species in the ground layer in 2005.

These changes appeared to reflect an overall shift in the presence and abundance of species in the Middlefork ground layer. To examine this, I calculated the percent similarity of the 50 ground layer plots between 1996 and 2005; the result was only 53.4% similarity between the two years. This indicates that species composition in the ground layer shifted rather markedly between 1996 and 2005.

Spatial Patterns in Savanna Ground Layer

A graph of the DCA ordination on the first two axes is shown in Figure 6. This graph displays a relatively large “spread”, or separation between the plots based on their relative species composition, especially along the first (x-) axis.

DCA ordination correlations with all environmental factors are presented in Table 7. Factors are listed in order of highest to lowest r^2 values for the first axis,

thus the table conveys a ranking of the relative strength of correlation between the various factors and ordination scores along the first and most important ordination axis. For assessing statistical significance, a Bonferroni adjustment was made to the significance level to maintain an experiment-wide significance level of $\alpha = 0.05$, and the resulting individual test significance level was 0.003.

The r^2 values (Table 7) for the first ordination axis indicate that percent open canopy ($r^2 = 0.437$, $p < 0.001$) was the most highly-correlated environmental parameter with the distribution of plots in species space. Nearly as highly-correlated were magnesium ($r^2 = 0.429$, $p < 0.001$), calcium ($r^2 = 0.426$, $p < 0.001$), and cation exchange capacity ($r^2 = 0.396$, $p < 0.001$). Next in importance was percent moisture (measured with a probe on August 28th; $r^2 = 0.376$, $p < 0.001$), followed by PAR as a percentage of full sun ($r^2 = 0.309$, $p < 0.001$), pH ($r^2 = 0.280$, $p < 0.001$), percent organic matter ($r^2 = 0.235$, $p < 0.001$) and potassium ($r^2 = 0.175$, $p \sim 0.003$). All of these significant correlations were positive. The horizontal lines in Figure 6 are layered onto the previously-derived ordination results to display graphically the association of the most highly-correlated environmental factors with the ordination results; all of these factors exhibit a strong alignment with the first axis. Other soil characteristics, including percent moisture on June 2nd, total phosphorus, percent clay, and total nitrogen, appeared to exhibit appreciable but only marginally significant correlations with axis one. In contrast, none of the measured environmental factors was highly correlated with the 2nd or 3rd axes.

The direct gradient analysis resulted in a visual array of species medians along the light gradient (Appendix 2). Ranking of species according to the decile in which their median canopy openness value falls and displaying the species medians by decile across the canopy openness gradient is presented in Figure 7.

For the CCA, the percent of variance in species data explained by each axis was 6.5, 2.8 and 2.3 percent for axes one through three, respectively, and the species-environment correlations for axes one through three were 0.969, 0.883 and 0.871. Monte Carlo test results indicated that the axis 1 correlation was statistically-significant ($p = 0.01$), whereas those for axes two and three were not.

DISCUSSION

Characterization of Savanna Vegetation, 2005

Classification of wooded communities based on percent canopy cover is a common, though arbitrary, practice designed more to facilitate the analysis of

these communities than to express any meaningful ecological distinctions (Curtis 1959). In the Midwest, terrestrial plant communities are properly characterized as elements along a continuum of prairie to savanna to woodland to forest. These elements intergrade and historically formed a matrix of interacting communities, each with a characteristic range in environmental conditions and dominant species. The common use of percent canopy cover to define savanna communities has been criticized due to the spatial heterogeneity of savanna trees (Leach and Givnish 1998); on a small scale the concept of an average percent canopy loses relevance given the heterogeneous nature of savanna tree arrangements. The use of average tree density is subject to this same limitation. Only when we view the landscape at a scale sufficient to represent the entirety of a habitat or natural area, do average percent canopy or tree density lend themselves to interpretation for classification purposes.

In this study, average tree density was 450 trees/ha. When this result is compared with less than 50 trees/ha as estimated by some for savanna tree density (Pruka 1994; Bowles and McBride 1996), the comparison suggests that the Unit One savanna at Middlefork does not fall within the bounds of the conventional savanna classification. However, almost two-thirds (62%) of the trees at Middlefork were in the smallest size class (5–15 cm dbh), and 93% were below 35 cm dbh. Only 30 trees/ha were recorded in the largest size class (> 55 cm dbh), a density that is consistent with common savanna classifications. The relative scarcity of large canopy trees in the Unit One savanna is an indication that historic conditions discouraged the growth of trees at their current densities. Many of the smaller trees were shagbark hickory saplings, a species that commonly fills canopy gaps in large numbers, but of which few individuals survive to attain larger sizes (Curtis 1959). In addition, although I did not collect percent canopy data for the tree community of the savanna, light availability as measured by both hemispherical canopy openness and PAR together with the presence of a relatively large number of prairie species in the ground layer indicate that the savanna still has sufficient availability of light to maintain compositional characteristics of a high-quality savanna. Furthermore, examination of the aerial photograph of the site in Figure 3 indicates that tree density in the western part of the Unit One savanna is greater than in the eastern half; thus placement of transects along the western half of the savanna by the original researchers at the site may have led to overestimation of tree density for the savanna.

Most studies of savannas have focused on canopy trees and the ground layer; however, savannas historically had a significant shrub layer that commonly

featured an abundance of *Corylus americana* and also oak “grubs” which were stunted by frequent fires (Curtis 1959; Bowles and McBride 1996; Anderson 1998). Although I encountered relatively few oaks in the shrub layer (5 stems/ha of all oak species combined), *C. americana* was the most abundant shrub at Middlefork in 2005 with 640 stems/ha. The relative scarcity of young oak recruits in the shrub layer is likely a result of competition from *Rhamnus cathartica* and other aggressive, invasive shrubs that were extremely abundant until relatively recently.

Many studies have documented high diversity in relatively undisturbed remnant savanna ground layers (Pruka 1994; Hujik 1995; Taft 1997; Leach and Givnish 1999). I also found the ground layer of the Unit One savanna at Middlefork to be unusually species-rich. Comparison of simple species richness at the site with that of other contemporary savanna studies in northern Illinois and southern Wisconsin indicates that species richness at Middlefork is as great or greater than other savannas in the region. For example, Leach and Givnish (1999) conducted an intensive study of relatively undisturbed remnant savanna ground layers at twelve sites of varying soil textures in southern Wisconsin; at each site, 50 to 100 1 m² quadrats were sampled. Mean plot richness in their study was 16.1 species (± 1.3 [mean \pm SD]) as compared with 17.3 for the current study. In a study of a remnant silt-loam savanna at the Wolf Road Prairie Nature Preserve in Cook County, Illinois, Bowles and McBride (1998) encountered 96 species in a total area sampled that was approximately 40% larger than what I sampled, in which I recorded 163 species. However, the Wolf Road site had suffered from decades of fire suppression which had allowed light availability to become dramatically reduced, whereas Middlefork has been fire-managed for several years. Pruka (1994) sampled 250 1 m² quadrats in a study of an upland oak savanna remnant in southwestern Wisconsin and encountered 119 species in a total area sampled of five times that in the current study. Hujik (1995) sampled 100 1 m² quadrats at each of three high-quality remnant savannas in southern Wisconsin and recorded 55, 67 and 88 species at the three sites, respectively.

Another means by which diversity may be compared among sites is by using beta diversity as a metric of compositional turnover. Whittaker (1972) proposed interpreting beta diversity as the number of times the species are replaced among the plots of a site. Beta diversity at Middlefork was 8.4, which compares favorably with Leach and Givnish (1999), who calculated an average beta diversity of 4.6 for upland savannas ($n = 9$) in southern Wisconsin (after adjustment to equate with my method of calculation). In the same study Leach and Givnish calculated an average beta diversity of 2.7 for upland prairies ($n =$

16) and 4.4 for upland forests ($n = 22$) in the same region; they suggested that the relatively lower beta diversity found within the prairie and forest sites may reflect lower microsite heterogeneity within those communities as compared with the savanna sites in their study. Applying this logic to my study, it is quite possible that Middlefork has relatively greater microsite heterogeneity than the other savannas against which I have compared it, and this may explain its high beta diversity relative to the other savannas. This interpretation is consistent with the wide range in light, soil moisture, and other environmental measurements that I recorded during my study.

Swink and Wilhelm (1994) developed a floristic quality index (FQI) for the Chicago region that is designed to be used to assess the relative conservation importance of natural areas in the region. Under their rating system, the floristic quality index of 53.2 that I calculated for the Unit One savanna at Middlefork falls within the range of FQI values representative of natural areas deemed extremely rare and of high conservation significance.

The dominance of forbs in the savanna at Middlefork is consistent with extensive recent studies of remnant savannas in southern Wisconsin (Leach and Givnish 1999). Leach and Givnish found most of the oak savannas they studied to be dominated by forbs, and that dominance of forbs is greater on silty soils, whereas grasses tend to be more abundant on sandy soils. These researchers also challenged earlier characterizations by Curtis (1959) and Bray (1960) that savannas are strictly dominated by grasses; Leach and Givnish attributed the characterization of Curtis and Bray to the fact that they were apparently biased toward selecting sites dominated by prairie grasses.

While there appears to be ample evidence that savanna ground layers are quite diverse when not subject to high levels of anthropogenic disturbance, considerable controversy nevertheless surrounds discussions of what constitutes a typical savanna ground layer flora, primarily because there are few high-quality remnants that can serve as reference sites. Specifically, researchers have debated whether savannas are mere ecotones between prairies and woodlands, and hence have a ground layer comprised simply of a combination of prairie and woodland species, or whether certain species are characteristic of savanna and thus may be considered as “indicators” of savanna (Curtis 1959; Bray 1960; Packard 1988, 1993; Anderson 1991; Mendelson et al. 1992; Leach and Givnish 1999). Indeed, in the effort to identify savanna indicator species, one is somewhat stymied by the fact that savannas share so many of their most important species with prairies or woodlands. This is to be expected if one considers the clumped distribution of trees in a savanna, with heavily shaded groves favoring

woodland species interspersed with openings dominated by prairie species. But most researchers on either side of this debate acknowledge that many species do appear to be modal, or at least characteristic, in savannas, hence it is reasonable to refer to these species as “characteristic savanna species”.

I found 26 species at Middlefork that are considered by various researchers to be characteristic of savannas (Table 8). Many of these species are by themselves ill-suited as definitive indicators of remnant savanna given that they may occur elsewhere; nevertheless, they may contribute critically to the identification of remnant savanna via a weight of evidence approach. Their value as indicators increases with the number of characteristic species found in a given location; thus, by recording or observing such a large number of characteristic savanna species, my data add to the growing body of literature that documents what may be regarded as a characteristic savanna flora. When used in combination with other indicators of savanna remnants such as large open-grown oaks, a diverse ground layer (in relatively undisturbed remnants; Leach and Givnish 1998) and perhaps multiple-stemmed oaks that have matured from oak grubs (Bowles and McBride 1996), this species list can help land managers and restorationists identify savanna remnants suitable for restoration, identify species suitable for seeding in local fine-soil savanna restorations, and provide a model for restoration projects. Middlefork thus represents an important reference site for the restoration and management of fine-textured soil oak savannas in the Chicago region and throughout the greater Midwest.

Temporal Change in Savanna Vegetation, 1996–2005

The density of trees increased from 390/ha to 450/ha at Middlefork between 1996 and 2005 (see Table 5 for raw counts), continuing the trend documented by Bowles et al. (2004) between 1986 and 1996. The continuing increase in tree density between 1996 and 2005 was mostly due to the continued increase in the number of 5–15 cm dbh stems of *Carya ovata* (Table 5). This trend raises an important management issue of the extent to which tree density should be reduced in order to maintain the site’s savanna characteristics.

Given that *Carya ovata* stems measuring 5–15 cm dbh now comprise 40% of total tree density in the Unit One savanna, management of this species is of particular concern for tree management in the savanna. An important management consideration is the extent to which *C. ovata* was present as a part of the presettlement tree community at Middlefork. Based on Moran’s (1978) assessment of the presettlement vegetation of Lake County (IL), and Public Land Survey (PLS) data recorded in the late 1830 s (N. Huber, pers.

comm.), it would appear that *C. ovata* was a characteristic member of the presettlement, oak-dominated savanna tree community at Middlefork.

Another important consideration in the management of *Carya ovata* is the frequency, coverage, and intensity of prescribed burns in the savanna. The Lake County Forest Preserve District had conducted prescribed burns in the savanna at Middlefork on five occasions over the previous ten years (Ken Klick, pers. comm.). These spring and fall burns covered between 80 and 100% of the unit, and were of moderate intensity. The continued increase in abundance of small trees despite frequent prescribed burns may be explained in at least two ways: 1) the presence of a relatively large number of small trees represents a natural, presettlement condition in the savanna, and is in part explained by recruitment of small, mostly short-lived *C. ovata*; or 2) the intensity of prescribed burns conducted in spring and fall has been lower than that of landscape-scale, presettlement fires, and thus prescribed burns have had relatively less ability to kill young trees. Bowles et al. (2004) suggested that prescribed burning during the growing season, when conditions are drier, should be conducted on an experimental basis. These fires may generate more heat and thus would have stronger effects on tree survival, and in this manner would have effects on vegetation that are more similar to those of historic fires. Of course, land managers would also need to consider impacts of dry-season fires on other components of the vegetation before implementing such an experiment.

In contrast to the apparent lack of response of the tree community to management, responses of the shrub layer to management have been much stronger. The dramatic decline in shrub layer stem density from 12,460 to 1,400 stems/ha between 1996 and 2005 represents a complete turnaround from the period 1986–1996, during which the density of shrub layer stems increased by 57.7% (Bowles et al. 2004). This surge in shrub layer stem density from 1986 to 1996, followed by an even more dramatic decline in stem density between 1996 and 2005, is due largely to the invasion (between 1986–1996), then control (during 1996–2005), of *Rhamnus cathartica*, for which stem density was reduced 99% from 5,680 to 60 stems/ha between 1996 and 2005. Other species of shrubs were also reduced, including targeted species such as *Lonicera tatarica* and *Cornus racemosa*. A non-target species, *Corylus americana*, also declined between 1996 and 2005, possibly as a result of changing environmental conditions on the site, by top-killing of shoots by a recent fire, or a combination of factors. The decline of *Corylus* abundance in the shrub layer was offset by an increase in *Corylus* abundance in the ground layer (mean percent cover increase from 0.6 to 2.0%), which may represent resprouting after fires.

As in the shrub layer, the ground layer responded positively to management between 1996 and 2005. Significant increases in species richness and in both diversity indices between 1996 and 2005 (refer to Table 4) are an indication that management is restoring the site in a manner consistent with management goals for the site. The combination of prescribed burns and removal of invasive species appears to be effectively restoring the savanna ground layer on a trajectory toward its presumed presettlement condition of relatively higher species richness and diversity. This positive result was achieved without seed distribution in the sampling area (K. Klick, pers. comm.).

While ground layer species richness and diversity increased between 1996 and 2005, at the same time there was a notable shift in species composition and abundance (percent similarity of 53.4%). Several invasive species warrant the attention of the Forest Preserve District: 1) *Phalaris arundinacea* exhibited a significant increase in mean plot cover (from 0.45 to 3.21%) and frequency (from three to nine plots); 2) *Solidago altissima* increased significantly in mean plot cover (from 3.2 to 6.6%) and has become the most abundant species in the ground layer; and 3) *Glechoma hederacea* L. (ground ivy), which was not recorded during 1996, occurred in two plots in 2005. Although populations of *Phalaris* and *Glechoma* are somewhat localized and could be readily controlled on the site, *S. altissima* is apparently adapted to fire and may require special management in order to prevent it from increasing further in abundance. In addition, two other invasive forbs, *Lythrum salicaria* and *Alliaria petiolata*, are present at low densities in the savanna but should be closely watched.

Spatial Patterns in Savanna Ground Layer

The results from the direct gradient analysis indicate that the high species richness in the savanna ground layer is in part attributable to the wide range in light levels and the broad distribution of ground layer species across the light gradient. The concentration of half of the species medians in the middle of the light gradient (Figure 7) is an indication that a large percentage of species are adapted to part-shade, part-sun conditions in the savanna at Middlefork. Other savanna researchers have also found a large percentage of species to be centrally-oriented along the middle of the light gradient (Bray 1958; Curtis 1959; Pruka 1994; Leach and Givnish 1999; Bowles et al. 2004). The other half of the species medians are divided between the most sunny or the most shaded deciles. Taken together, these patterns confirm the importance of a wide range of light availability in promoting diversity in the savanna ground layer.

A scan of Appendix 2 reveals additional insight as to the nature of species distributions in the savanna

ground layer along the light gradient. For example, most of the species at the extremes are narrowly restricted to either open-canopy, sunny habitats (such as mesic prairies, wet prairies and sedge meadows), or to more closed canopy habitats associated with woodlands; these species were primarily recorded within a narrow range at either end of the light gradient. Examples of open-canopy species included *Eryngium yuccifolium* Michx., *Parthenium integrifolium* Britton, *Silphium terebinthinaceum* Michx., *Hypoxis hirsuta* (L.) Coville, *Carex buxbaumii* Whalenb., *Calamagrostis canadensis* (Michx.) P. Beauv., and *Galium obtusum* Bigelow. Characteristic woodland species tended to be somewhat less restricted on the other end of the light gradient, and included *Smilacina racemosa* (L.) Desf., *Geum canadense* Jacq., *Hydrophyllum virginianum* L., *Asclepias exaltata* L., *Carex cephalophora* Willd., and *Allium cernuum* Roth.

Species whose distributions were centered in the middle of the light gradient not only tended to be more abundant; but also tended to exhibit a much wider distribution across the light gradient. Examples included *Fragaria virginiana* Duchesne, *Solidago altissima*, *S. Juncea* Aiton, *Tradescantia ohimensis* Raf., *Rosa carolina* L., and *Smilax* spp. These species appear to be more adapted to a broad range of light availability than the species at the extremes. Pruka (1994) also found a large proportion of savanna ground layer species to exhibit a wide distribution across the light gradient. The fact that many species' distributions are centered in the middle range of the light gradient suggests that they may be adapted to savanna conditions; this would support the contention of Packard (1993) that many characteristic savanna species in this group are modal in savannas. Many of the characteristic species listed in Table 8 have distributions that are centered in the middle of the light gradient, which supports this position.

Savanna researchers have theorized that soils should hold more moisture under tree canopies than in the open given the reduced evapotranspiration that occurs under tree canopies (Ko and Reich 1993). However, I obtained the seemingly counterintuitive result that percent canopy openness was positively and significantly correlated with soil moisture; this result was consistent regardless of how (two methods) or when (three different occasions) I measured soil moisture. A relevant site-specific factor that may explain this is the fact that most of the open-canopy areas at Middlefork occur in sedge meadows or wet prairies, wet habitats of low topographical position which have far greater moisture-retaining capacities than upland areas. This heterogeneity in soil classifications at Middlefork may also underlie other observed gradients, since percent organic matter, pH, cation exchange capacity, calcium and magnesium,

were all positively and significantly related to canopy openness. This result contrasts with the findings of Dahlgren et al. (1997), who found that organic matter, pH, calcium and magnesium were higher under oak canopies (in clay loam soils with some gravel) than in the adjacent grasslands. Ko and Reich (1993) also found organic matter to be higher under oak trees than under adjacent grassland (on sites with sandy loam or silt loam soils), but found pH to be lower under oaks. Ko and Reich (1993) also noted that loam soils in their study had higher pH, organic matter, calcium and magnesium than sandy soils under similar management histories; this suggests that the ability to generalize about relationships between light and soil among sites may be limited by differences in soil texture. Perhaps an even greater limitation on light and soil comparisons among sites is the heterogeneity of soils present at Middlefork, from moist wetland soils to moderately-drained upland soils. It appears that this heterogeneity of soil types may override the localized effect of tree canopies on soil characteristics.

By definition, a savanna is characterized by spatially heterogeneous environmental conditions given the irregular distribution of trees and various resources/physical factors. The unique diversity of natural communities at Middlefork accentuates this characteristic, with groves of trees interspersed with sedge meadows and wet prairies. The spatial heterogeneity hypothesis holds that local plant diversity is enhanced by heterogeneity in the spatial distribution of resources and physical factors (Tilman and Pacala 1993). Under this hypothesis, each plant species is assumed to possess an optimal combination of physical factors and resources to which it is best suited; thus, the more variety in these factors, and combinations of them, the more opportunities for species coexistence. The diversity of species at Middlefork, and the patterns of species distributions detected along the light gradient, support the spatial heterogeneity hypothesis. The result of the wide range in light availability across the savanna is that a wide array of species are present in the ground layer, including woodland species, species that are at home in part-sun, part-shade, and prairie species. Significant correlations between the first ordination axis and other environmental parameters suggests that these additional factors may further influence the diversity of the ground layer through heterogeneity in the distribution of these resources and conditions. Thus, the size of the species pool is much greater than a community not possessing the same level of habitat diversity.

The evidence that spatial heterogeneity in environmental conditions enhances species diversity in the savanna holds implications for management of the savanna, most directly with respect to the management of woody plants in the shrub layer. The previous

domination of *Rhamnus cathartica* and other invasive shrubs would have reduced light throughout much of the savanna and restricted the light gradient, and the increase in richness of the ground layer at Middlefork since 1996 may be due in part to the release from this light suppression. In their study at Wolf Road Savanna, Bowles and McBride (1998) documented the negative effect of a restricted light gradient due to invasive shrubs and increased tree densities on species richness in the ground layer. Implications of spatial heterogeneity for the management of the tree community at Middlefork seem less obvious; the increase in species diversity of the savanna ground layer since 1996 in step with an increase in tree density suggests that current light availability is sufficiently heterogeneous to support a diverse ground layer flora. Future management of the savanna should include periodic measurement of light levels to assess change in ground layer diversity relative to changes in light availability. Heterogeneity in soil parameters such as moisture, organic matter and nutrients seems to be driven by the natural diversity of community types, and appears less directly linked with management actions.

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LITERATURE CITED

- Anderson, R. C. 1983. The eastern prairie-forest transition — an overview. pp. 86–92 in: R. Brewer, ed., Proceedings of the Eighth North American Prairie Conference. Western Michigan University, Kalamazoo.
- Anderson, R. C. 1991. Savanna concepts revisited. *Bioscience* 41(6):371 pp.
- Anderson, R. C. 1998. Overview of Midwestern oak savanna. *Transactions of the Wisconsin Academy of Sciences, Arts and Letters* 86:1–18.
- Bray, J. R. 1958. The distribution of savanna species in relation to light intensity. *Canadian Journal of Botany* 36:671–681.
- Bray, J. R. 1960. The composition of savanna vegetation in Wisconsin. *Ecology* 41(4):721–732.
- Bowles, M. L. and J. L. McBride. 1996. Evaluation and classification of savanna, woodland and barrens natural areas in northern Illinois. The Morton Arboretum, Lisle, IL. 21 pp.
- Bowles, M. L. and J. L. McBride. 1998. Vegetation composition, structure, and chronological change in a decadent Midwestern North American savanna remnant. *Natural Areas Journal* 18(1):14–27.
- Bowles, M., J. McBride, S. Apfelbaum, A. Haney, and S. Packard. 2004. Vegetation composition, structure, and temporal change in a Midwestern silt-loam mesic savanna. Unpublished manuscript.
- Brower, J. E., J. H. Zar, and C. N. von Ende. 1998. *Field and Laboratory Methods for General Ecology*. 4th ed. WCB/McGraw-Hill.
- Chicago Region Biodiversity Council. 1999. *Biodiversity Recovery Plan*.
- Curtis, J. T. 1959. *The vegetation of Wisconsin: an ordination of plant communities*. University of Wisconsin Press, Madison. 657 pp.
- Dahlgren, R. A., M. J. Singer, and X. Huang. 1997. Oak tree and grazing impacts on soil properties and nutrients in a California oak woodland. *Biogeochemistry* 39:45–64.
- Frazer, G. W., C. D. Canham, and K. P. Lertzman. 1999. *Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-color fisheye photographs, users manual and program documentation*. Simon Frazer University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.
- Hipp, A. 1998. A checklist of Carices for prairies, savannas, and oak woodlands of southern Wisconsin. *Transactions of the Wisconsin Academy of Sciences, Arts, and Letters* 86:77–99.
- Hujik, P. M. 1995. *Lowland savannas: groundlayer composition and distribution in relation to elevation and light*. Thesis. University of Wisconsin, Madison.
- Jennings, S. B., N. D. Brown, and D. Sheil. 1999. Assessing forest canopies and understory illumination: canopy closure, canopy cover and other measures. *Forestry* 72(1):59–73.
- Kilburn, P. D. 1959. The forest-prairie ecotone in northeastern Illinois. *American Midland Naturalist* 62:206–217.
- Ko, L. J. and P. B. Reich. 1993. Oak tree effects on soil and herbaceous vegetation in savannas and pastures in Wisconsin. *American Midland Naturalist* 130:31–42.
- Krebs, C. J. 1999. *Ecological methodology*. Second edition. Benjamin/Cummings, Menlo Park, CA. 620 pp.
- Leach, M. K. 1996. *Gradients in groundlayer composition, structure and diversity in remnant and experimentally restored oak savannas*. Dissertation. University of Wisconsin, Madison.

- Leach, M. K. and T. J. Givnish. 1998. Identifying highly restorable savanna remnants. *Transactions of the Wisconsin Academy of Sciences, Arts and Letters* 86:119–127.
- Leach, M. K. and T. J. Givnish. 1999. The ecology of oak savanna ground layers. *Ecological Monographs* 69(3):353–374.
- Leach, M. K. and L. Ross. 1995. Oak ecosystem recovery plan. U.S. Environmental Protection Agency, Great Lakes National Program Office, Chicago, and The Nature Conservancy. 112 pp.
- Mendelson, J., S. P. Aultz, and J. D. Mendelson. 1992. Carving up the woods – savanna restoration in northeastern Illinois. *Restoration and Management Notes* 10:127–131.
- McCune, B. and M. J. Mefford. 1999. PC-ORD. Multivariate analysis of ecological data, Version 4. MJM Software Design, Gleneden Beach, Oregon, USA.
- Moran, R. C. 1978. Presettlement vegetation of Lake County, Illinois. pp. 12–18 in: *Proceedings of the Fifth Midwest Prairie Conference*, D. D. Glenn-Lewin and R. Q. Landers, eds. Iowa State University, Ames.
- Nuzzo, V. A. 1986. Extent and status of Midwest oak savanna: presettlement and 1985. *Natural Areas Journal* 6(2):6–36.
- Packard, S. 1988. Just a few oddball species: restoration and the rediscovery of the tallgrass savanna. *Restoration and Management Notes* 6:13–22.
- Packard, S. 1993. Restoring oak ecosystems. *Restoration and Management Notes* 11:5–16.
- Pruka, B. W. 1994. Distribution of understory plant species along light and soil depth gradients in an upland oak savanna remnant in southern Wisconsin. Thesis. University of Wisconsin, Madison.
- Pruka, B. W. 1995. Indicator plant species of recoverable oak savannas and open oak woodlands in southern Wisconsin. Appendix D, *Proceedings of the 1995 Midwest Oak Savanna and Woodland Ecosystems Conference*. <http://www.epa.gov/glnpo/ecopage/upland/oak/oak95/app-d.htm>.
- Schwegman, J. 1973. Comprehensive plan for the Illinois Nature Preserves System. Part 2: The Natural Divisions of Illinois. Illinois Nature Preserves Commission.
- Swink, F. and G. Wilhelm. 1994. *Plants of the Chicago Region*. 4th ed. Indiana Academy of Sciences, Indianapolis.
- Taft, J. B. 1997. Savanna and open woodland communities. pp. 24–54 in: M. W. Schwartz, ed., *Conservation in Highly Fragmented Landscapes*. Chapman and Hall, New York.
- Tilman, D. and S. Pacala. 1993. The maintenance of species richness in plant communities. *In*: R. E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities: historical and geographical perspectives*. The University of Chicago Press, 13–25.
- White, J. 1978. Classification of natural communities in Illinois. Illinois Natural Areas Inventory Technical Report. Illinois Natural Areas Inventory, Urbana.
- Whittaker, R. H. 1972. Evolution and measurement of species diversity. *Taxon* 21(2/3):213–251.

Table 1: Spearman rank correlations between ground layer abundance as measured using percent cover vs. dm² frequency methods. Degrees of freedom = 162 for species and 49 for all other correlations.

Correlation	r _s	r ²	p-value*
Species	.860	0.740	< 0.001
Plots	.528	0.279	< 0.001
Exp. Shannon diversity	.850	0.722	< 0.001
Inv. Simpson diversity	.669	0.448	< 0.001
Shannon evenness	.592	0.350	< 0.001
Simpson evenness	.429	0.184	= 0.002

*=p-values are all significant (i.e. all are below Bonferroni-adjusted significance level of 0.05/6 = 0.008).

Table 3: Shrub layer survey results for Unit One, Middlefork Savanna, 2005. Total area sampled is 500 m².

Species	Total Stems	Stems/ha
<i>Corylus americana</i>	32	640
<i>Cornus racemosa</i>	11	220
<i>Spiraea alba</i>	6	120
<i>Fraxinus americana</i>	5	100
<i>Quercus coccinea</i>	4	80
<i>Lonicera tatarica</i>	3	60
<i>Rhamnus cathartica</i>	3	60
<i>Rubus occidentalis</i>	3	60
<i>Fraxinus pennsylvanica</i>	1	20
<i>Quercus macrocarpa</i>	1	20
<i>Rhamnus frangula</i>	1	20
Total	70	1400

Table 2: Tree survey results for Unit One, Middlefork Savanna, 2005. Total area sampled is 1000 m².

Raw Counts	Size Classes (cm)					Exact dbh	Density
	5 to 15	> 15–35	>35–55	>55			
<i>Carya ovata</i>	18						18
<i>Fraxinus americana</i>	1	1					2
<i>Quercus alba</i>					1	66	1
<i>Q. ellipsoidalis</i>	6	11					17
<i>Q. macrocarpa</i>	3	1		1		75	5
<i>Q. rubra</i>		1		1		58	2
Total	28	14	0	3			45

Per Hectare	Density	RD	Basal area	RBA	IV
<i>Carya ovata</i>	180	40.00	1.41	7.23	23.62
<i>Fraxinus americana</i>	20	4.44	0.57	2.91	3.68
<i>Quercus alba</i>	10	2.22	3.42	17.50	9.86
<i>Q. ellipsoidalis</i>	170	37.78	5.87	30.03	33.90
<i>Q. macrocarpa</i>	50	11.11	5.14	26.31	18.71
<i>Q. rubra</i>	20	4.44	3.13	16.02	10.23
Total	450	100.00	19.54	100.00	100.00

Table 4: Richness, diversity, and evenness indices for the ground layer of Unit One, Middlefork Savanna, 1996 and 2005. Standard error of mean values are in parentheses.

	1996	2005
Site		
Species Richness	156	163
Native Species Richness	135	140
Non-Native Species Richness	21	23
Jackknifed Species Richness	204	209
Exponential Shannon's Diversity Index	13.71 (+ 0.72)	15.87 (+ 0.62)
Inverse of Simpson's Diversity Index	12.09 (± 0.76)	14.30 (± 0.67)
Shannon's Evenness Index	0.95 (± 0.01)	0.96 (± 0.01)
Simpson's Evenness Index	0.79 (± 0.03)	0.81 (± 0.02)
Floristic Quality Index	53.5	53.2
Beta diversity	9.2	8.4
Plot		
Mean Plot Total Species Richness	15.36 (+ 0.69)	17.3 (+ 0.57)
Mean Plot Native Species Richness	13.18 (+ 0.62)	14.3 (+ 0.45)
Mean Plot Non-native Species Richness	2.16 (+ 0.21)	3.0 (+ 0.29)
Growth Forms, Mean Plot Percent Cover		
Forbs	not recorded	41.5% (+ 2.22)
Graminoids	not recorded	25.6% (+ 3.05)
Woody Plants	not recorded	14.4% (+ 2.07)

Table 5: Tree densities by size class for Unit One, Middlefork Savanna, 1996 and 2005. Data are actual counts per 1000 m² of sampling area.

1996		Size Class			
Taxon	5 to 15	>15-35	>35-55	>55	
<i>Carya ovata</i>	4	1	1		
<i>Populus tremuloides</i>	1				
<i>Quercus alba</i>	1			1	
<i>Q. ellipsoidalis</i>	5	12	1	1	
<i>Q. macrocarpa</i>	2	2		1	
<i>Q. rubra</i>		1		1	
<i>Rhamnus cathartica</i>	3	1			
SUM	16	17	2	4	
2005		Size Class			
Taxon	5-15	> 15-35	>35-55	>55	
<i>Carya ovata</i>	18				
<i>Fraxinus americana</i>	1	1			
<i>Quercus alba</i>				1	
<i>Q. ellipsoidalis</i>	6	11			
<i>Q. macrocarpa</i>	3	1		1	
<i>Q. rubra</i>		1		1	
SUM	28	14	0	3	

Table 6: Shrub layer stem counts per hectare for Unit One, Middlefork Savanna, 1996 and 2005. Total area sampled is 500 m².

Species	1996 Stems/ha	2005 Stems/ha
<i>Rhamnus cathartica</i>	5680	60
<i>Cornus racemosa</i>	3720	220
<i>Corylus Americana</i>	1200	640
<i>Lonicera tatarica</i>	640	60
<i>Quercus ellipsoidalis</i>	300	80
<i>Fraxinus Americana</i>	260	100
<i>Carya ovata</i>	260	0
<i>Rosa multiflora</i>	100	0
<i>Prunus serotina</i>	40	0
<i>Populus tremuloides</i>	40	0
<i>Rhus glabra</i>	40	0
<i>Rosa sp.</i>	40	0
<i>Vitis sp.</i>	40	0
<i>Salix sp.</i>	40	0
<i>Quercus macrocarpa</i>	20	20
<i>Carya sp.</i>	20	0
<i>Quercus rubra</i>	20	0
<i>Spiraea alba</i>	0	120
<i>Rubus occidentalis</i>	0	60
<i>Fraxinus pennsylvanica</i>	0	20
<i>Rhamnus frangula</i>	0	20
Total	12,460	1,400

Table 7: Spearman rank correlations between DCA ordination scores and environmental factors for Middlefork Savanna, 2005.

Parameter	Axis 1			Axis 2			Axis 3		
	r_s	r^2	p-value	r_s	r^2	p-value	r_s	r^2	p-value
% Open Canopy	0.661	0.437	<0.001	0.115	0.013	>0.20	0.149	0.022	>0.20
Mg	0.655	0.429	<0.001	0.154	0.024	>0.20	0.015	0.000	>0.50
Ca	0.653	0.426	<0.001	0.165	0.027	>0.20	0.008	0.000	>0.50
Cation Exchange	0.629	0.396	<0.001	0.151	0.023	>0.20	0.081	0.007	>0.50
% Moisture (8/28)	0.613	0.376	<0.001	0.172	0.030	>0.20	0.023	0.001	>0.50
PAR as % Full Sun	0.556	0.309	<0.001	0.029	0.001	>0.50	0.198	0.039	>0.10
pH	0.529	0.280	<0.001	0.113	0.013	>0.20	0.122	0.015	>0.20
% Organic	0.485	0.235	<0.001	0.265	0.070	>0.05	0.036	0.001	>0.50
K	0.418	0.175	~0.003	0.257	0.066	>0.05	0.016	0.000	>0.50
P	0.396	0.157	~0.005	0.091	0.008	>0.50	0.059	0.003	>0.50
% Clay	0.393	0.154	=0.005	0.031	0.001	>0.50	0.220	0.048	>0.10
N ^a	0.376	0.141	>0.005	0.127	0.016	>0.50	0.263	0.069	>0.10
% Moisture (6/2)	-0.337	0.114	>0.01	0.111	0.012	>0.20	0.250	0.063	>0.05
Temperature (7/24)	-0.325	0.106	>0.02	0.234	0.055	~0.10	0.207	0.043	>0.10
Temperature (6/5)	0.292	0.085	>0.02	0.123	0.015	>0.20	0.061	0.004	>0.50
% Sand	-0.263	0.069	>0.05	0.008	0.000	>0.50	0.056	0.003	>0.50
% Silt+Clay	0.245	0.060	>0.05	0.015	0.000	>0.50	0.048	0.002	>0.50
% Silt	-0.168	0.028	>0.20	0.140	0.020	>0.20	0.247	0.061	>0.05

p-value is significant at the Bonferroni-adjusted significance level of $\alpha = 0.05/18 = 0.003$; significance indicated in bold. Total nitrogen is based on 30 plots.

Table 8: List of characteristic savanna species in the ground layer of Unit One, Middlefork Savanna, 2005. Species are listed if they were recorded or observed at Middlefork and are represented in the literature as being characteristic of savanna. A suspected modality of a species in savanna, or a shared distribution of a species in prairies or woodlands, is indicated in the second column. Note that many of the species listed may be modal in savannas even if common in other communities. This list is limited to species considered “conservative”, i.e. requiring of some degree of habitat integrity; generally, a coefficient of conservatism of at least 5, see Swink and Wilhelm (1994).

Scientific Name	Primary Community(ies)	Reference
<i>Agastache nepetoides</i>	Savanna, woodland	Pruka (1995)
<i>Arenaria lateriflora</i>	Savanna, dry to mesic woodland	Bowles et al. 2(004)
<i>Asclepias purpurascens*</i>	Savanna	Packard (1988); Pruka (1995); Taft (1997)
<i>Aureolaria grandiflora*</i>	Savanna, woodland	Packard (1993); Pruka (1995); Taft (1997)
<i>Carex bebbii</i>	Lowland savanna, wet prairie, fens	Hipp (1998)
<i>Carex normalis</i>	Mesic savanna, wet prairie	Swink and Wilhelm (1994); Hipp (1998)
<i>Carex pensylvanica</i>	Savanna	Swink and Wilhelm (1994); Taft (1997); Hipp (1998); Bowles et al. (2004)
<i>Carex tenera</i>	Wet to mesic savanna, prairie	Swink & Wilhelm (1994), Hipp (1998)
<i>Coreopsis tripteris</i>	Savanna, woodland, prairie	Bowles et al. (2004)
<i>Corylus americana</i>	Savanna, woodland	Curtis (1959); White (1978); Taft (1997)
<i>Dodecatheon meadia</i>	Savanna, prairie, fen	Swink and Wilhelm (1994); Pruka (1995); Taft (1997)
<i>Elymus villosus*</i>	Savanna, woodland	Packard (1988); Pruka (1995)
<i>Gentiana flavida</i>	Savanna, prairie	Packard (1988); Pruka (1995); Taft (1997); Bowles et al. (2004)
<i>Helianthus divaricatus</i>	Savanna, woodland	Taft (1997); Bowles et al. (2004)
<i>Histrix patula</i>	Savanna, woodland	Packard (1988)
<i>Hypoxis hirsuta</i>	Savanna, prairie, calcareous meadow	Pruka (1995)
<i>Lathyrus ochroleucus**</i>	Savanna, dry woodland	Taft (1997); Bowles et al.(2004)
<i>Panicum latifolium</i>	Savanna, mesic woodlands	Packard (1988)
<i>Parthenium integrifolium</i>	Savanna, prairie	White (1978)
<i>Prenanthes alba</i>	Savanna, woodland	Pruka (1995)
<i>Silene stellata</i>	Dry savanna, woodland, prairie	White (1978); Packard (1988); Pruka (1995); Taft (1997); Bowles et al. (2004)
<i>Smilax lasioneura</i>	Savanna, woodland	White (1978), Bowles et al. (2004)
<i>Solidago ulmifolia</i>	Savanna, woodland	Packard (1988)
<i>Taenidia integerrima</i>	Savanna, woodland	Pruka (1995); Taft (1997)
<i>Veronicastrum virginicum</i>	Savanna, woodland, prairie	Pruka (1995); Taft (1997); Bowles et al. (2004)
<i>Zizia aurea</i>	Dry savanna, moist woodland, prairie	White (1978); Pruka (1995)

* Seen but not recorded in plots, or ** reported by others at the site.



Figure 1. Middlefork Savanna is located in Lake County, Illinois.

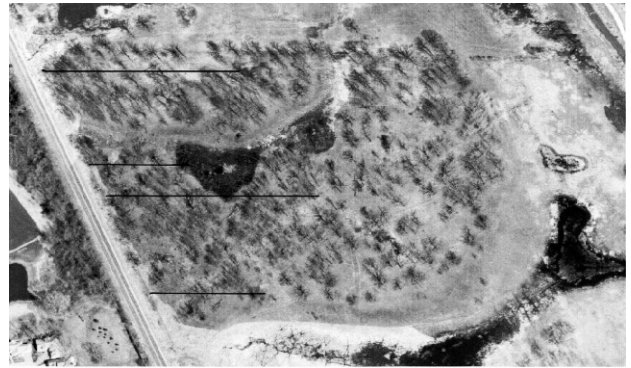


Figure 3. Close-up of Unit One savanna at Middlefork Savanna. Black lines show transect locations.

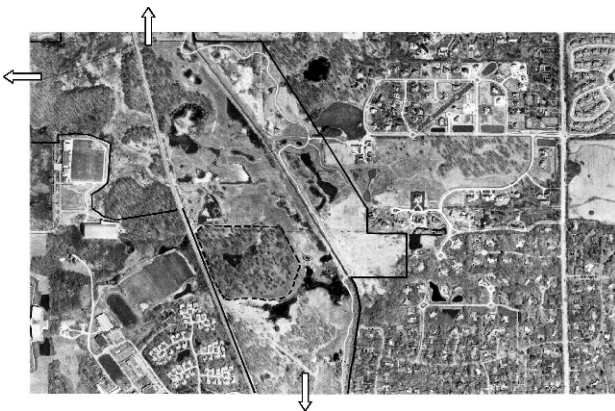


Figure 2. Aerial view of central part of Middlefork Savanna, Lake Forest, Illinois. Site boundary is outlined with solid black line and extends outside the photograph to the N, W and S as indicated by the arrows; Unit One study unit is within dotted line east of rail line. Site boundary is approximate.

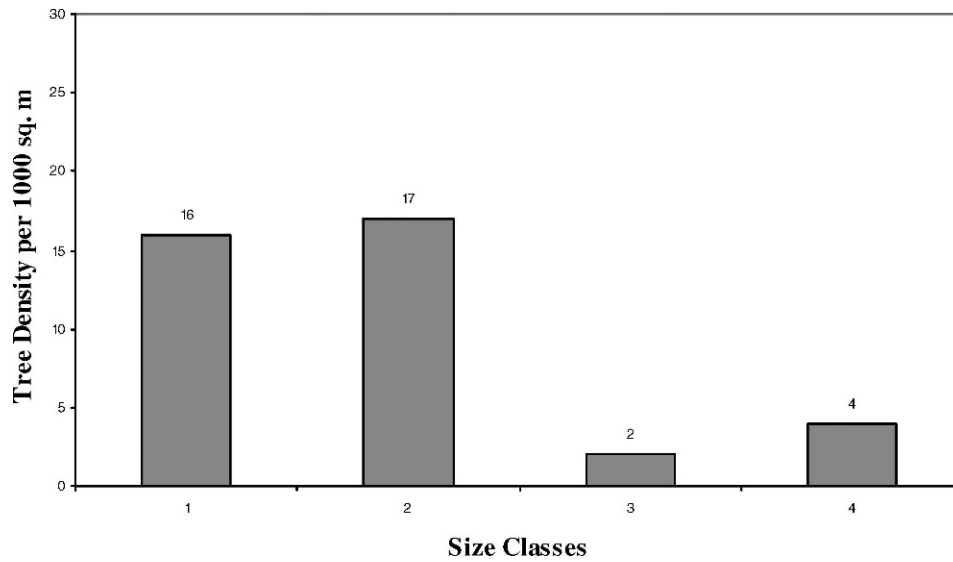


Figure 4. Middlefork Savanna Tree Community Structure, 1996. Values on y-axis represent actual tree counts in the sampled area. Size classes: 1 = 5–15 cm, 2 = 15–35 cm, 3 = 35–55 cm, and 4 = > 55 cm dbh.

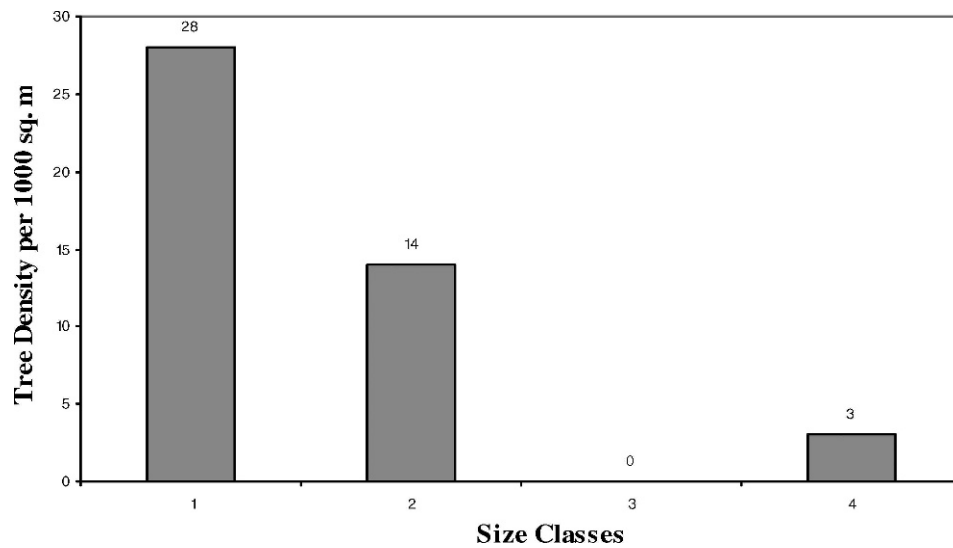


Figure 5. Middlefork Savanna Tree Community Structure, 2005. Values on y-axis represent actual tree counts in the sampled area. Size classes: 1 = 5–15 cm, 2 = 15–35 cm, 3 = 35–55 cm, and 4 = > 55 cm dbh.

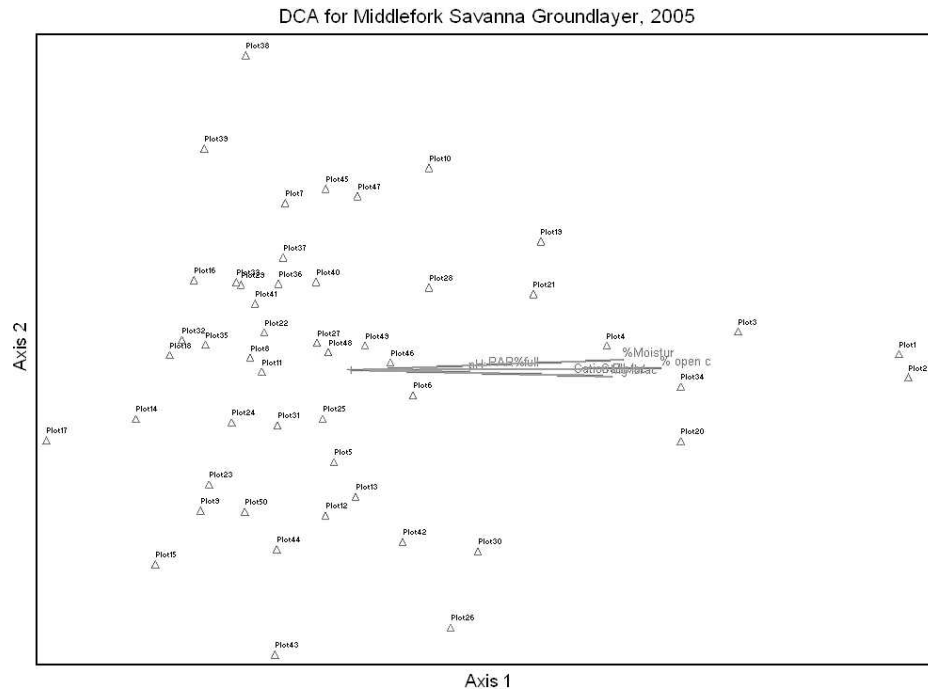


Figure 6. Scatterplot of detrended correspondence analysis ordination of round layer plots in species space, Unit One, Middlefork Savanna, 2005. Horizontal lines are layered onto the previously-derived ordination results to display the association of the most highly-correlated environmental factors with the ordination results.

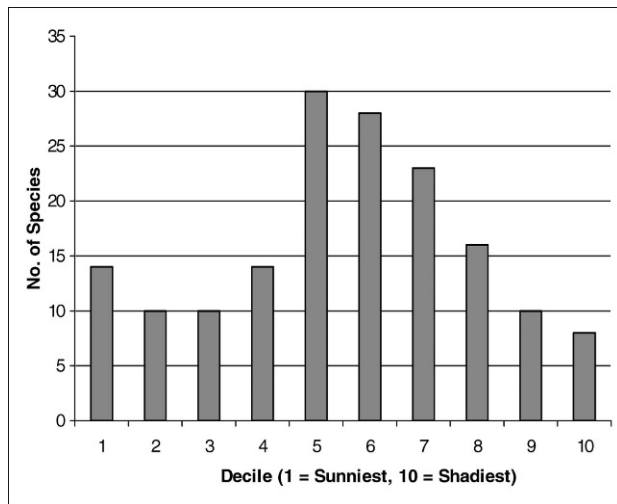


Figure 7. Frequency distribution of species medians across light gradient. Light gradient is divided into ten deciles; 1 = sunniest, 10 = shadiest.

APPENDIX 1:

Mean plot cover and plot frequency for all ground layer species recorded at Unit One, Middlefork Savanna, 2005.

Mean Plot Cover			Plot Frequency	
Taxon	mean	±s.e.m.	Taxon	freq
<i>Solidago altissima</i>	6.60	0.91	<i>Solidago altissima</i>	30
<i>Helianthus divaricatus</i>	5.61	1.31	<i>Taraxacum officinale</i>	30
<i>Taraxacum officinale</i>	4.50	0	<i>Potentilla simplex</i>	26
<i>Rhamnus cathartica</i>	4.20	0.87	<i>Smilax sp.</i>	25
<i>Potentilla simplex</i>	3.90	0	<i>Aster simplex</i>	23
<i>Cornus racemosa</i>	3.75	0.64	<i>Tradescantia ohioensis</i>	23
<i>Smilax sp.</i>	3.75	0	<i>Fragaria virginiana</i>	22
<i>Tradescantia ohioensis</i>	3.45	0	<i>Cornus racemosa</i>	21
<i>Fragaria virginiana</i>	3.30	0	<i>Helianthus divaricatus</i>	21
<i>Phalaris arundinacea</i>	3.21	1.60	<i>Rosa carolina</i>	21
<i>Rosa carolina</i>	3.15	0	<i>Veronicastrum virginicum</i>	21
<i>Veronicastrum virginicum</i>	3.15	0	<i>Rhamnus cathartica</i>	20
<i>Calamagrostis canadensis</i>	3.07	2.98	<i>Aster lateriflorus</i>	19
<i>Rubus pensilvanicus</i>	3.06	1.60	<i>Poa pratensis</i>	16
<i>Sphenophilus intermedia</i>	3.00	0.72	<i>Solidago juncea</i>	16
<i>Aster lateriflorus</i>	2.85	0	<i>Sphenophilus intermedia</i>	16
<i>Eleocharis elliptica</i>	2.82	2	<i>Geranium maculatum</i>	15
<i>Poa pratensis</i>	2.70	0.53	<i>Monarda fistulosa</i>	14
<i>Solidago juncea</i>	2.70	0.53	<i>Agrostis alba</i>	13
<i>Agrostis alba</i>	2.55	0.80	<i>Agrimonia gryposepala</i>	11
<i>Aster simplex</i>	2.40	1.02	<i>Carex tenera</i>	11
<i>Geranium maculatum</i>	2.25	0	<i>Circaea lutetiana canadensis</i>	11
<i>Monarda fistulosa</i>	2.10	0	<i>Poa compressa</i>	11
<i>Corylus americana</i>	2.01	1.93	<i>Viola sororia</i>	11
<i>Carex tenera</i>	1.95	0.64	<i>Anemone quinquefolia</i>	10
<i>Carex normalis</i>	1.86	1.65	<i>Cirsium arvensis</i>	10
<i>Agrimonia gryposepala</i>	1.65	0	<i>Rubus pensilvanicus</i>	10
<i>Circaea lutetiana canadensis</i>	1.65	0	<i>Bidens sp.</i>	9
<i>Poa compressa</i>	1.65	0	<i>Oxalis sp.</i>	9
<i>Viola sororia</i>	1.65	0	<i>Phalaris arundinacea</i>	9
<i>Anemone quinquefolia</i>	1.50	0	<i>Zizia aurea</i>	9
<i>Carex pensylvanica</i>	1.50	0.75	<i>Carex normalis</i>	8
<i>Cirsium arvensis</i>	1.50	0	<i>Carex pensylvanica</i>	8
<i>Aster sp.</i>	1.35	0	<i>Geum canadensis</i>	8
<i>Bidens sp.</i>	1.35	0	<i>Oxypolis rigidior</i>	8
<i>Oxalis sp.</i>	1.35	0	<i>Calamagrostis canadensis</i>	7
<i>Pycnanthemum virginianum</i>	1.35	0.80	<i>Daucus carota</i>	7
<i>Zizia aurea</i>	1.35	0	<i>Phleum pratense</i>	7
<i>Aster praealtus</i>	1.35	0.80	<i>Pycnanthemum virginianum</i>	7
<i>Onoclea sensibilis</i>	1.26	1.8	<i>Stachys tenuifolia hispida</i>	7
<i>Geum canadensis</i>	1.20	0	<i>Aster praealtus</i>	7
<i>Oxypolis rigidior</i>	1.20	0	<i>Allium canadensis</i>	6
<i>Daucus carota</i>	1.05	0	<i>Aster saggitifolius</i>	6
<i>Galium obtusum</i>	1.05	0.95	<i>Coreopsis tripteris</i>	6
<i>Phleum pratense</i>	1.05	0	<i>Festuca elatior</i>	6
<i>Stachys tenuifolia hispida</i>	1.05	0	<i>Hystrix patula</i>	6
<i>Allium canadensis</i>	0.90	0	<i>Smilacina racemosa</i>	6
<i>Aster saggitifolius</i>	0.90	0	<i>Arenaria lateriflora</i>	5

APPENDIX 1:
Continued.

Mean Plot Cover			Plot Frequency	
Taxon	mean	±s.e.m.	Taxon	freq
<i>Carex stricta</i>	0.90	0	<i>Corylus americana</i>	5
<i>Coreopsis tripteris</i>	0.90	0	<i>Elymus virginicus</i>	5
<i>Festuca elatior</i>	0.90	0	<i>Fraxinus sp.</i>	5
<i>Hystrix patula</i>	0.90	0	<i>Galium obtusum</i>	5
<i>Ranunculus septentrionalis</i>	0.90	1.06	<i>Sanicula marilandica</i>	5
<i>Smilacina racemosa</i>	0.90	0	<i>Senecio aureus</i>	5
<i>Arenaria lateriflora</i>	0.75	0	<i>Solidago ulmifolia</i>	5
<i>Elymus virginicus</i>	0.75	0	<i>Carex sp.</i>	4
<i>Fraxinus sp.</i>	0.75	0	<i>Juncus tenuis</i>	4
<i>Sanicula marilandica</i>	0.75	0	<i>Lycopus americanus</i>	4
<i>Senecio aureus</i>	0.75	0	<i>Prenanthes alba</i>	4
<i>Solidago gigantea</i>	0.75	1.22	<i>Ranunculus septentrionalis</i>	4
<i>Solidago ulmifolia</i>	0.75	0	<i>Thalictrum dasycarpum</i>	4
<i>Carex sp.</i>	0.60	0	<i>Achillea millefolium</i>	3
<i>Carex lacustris</i>	0.60	1.5	<i>Aquilegia canadensis</i>	3
<i>Carya ovata</i>	0.60	1.5	<i>Aster sp.</i>	3
<i>Juncus tenuis</i>	0.60	0	<i>Aster novae-angliae</i>	3
<i>Lycopus americanus</i>	0.60	0	<i>Carex molesta</i>	3
<i>Prenanthes alba</i>	0.60	0	<i>Carex pellita</i>	3
<i>Silphium terebinthinaceum</i>	0.60	1.5	<i>Cerastium vulgatum</i>	3
<i>Thalictrum dasycarpum</i>	0.60	0	<i>Comandra umbellata</i>	3
<i>Achillea millefolium</i>	0.45	0	<i>Elymus canadensis</i>	3
<i>Aquilegia canadensis</i>	0.45	0	<i>Equisetum arvense</i>	3
<i>Aster novae-angliae</i>	0.45	0	<i>Galium asprellum</i>	3
<i>Carex molesta</i>	0.45	0	<i>Hackelia virginiana</i>	3
<i>Carex pellita</i>	0.45	0	<i>Helianthus grosseserratus</i>	3
<i>Cerastium vulgatum</i>	0.45	0	<i>Juncus dudleyi</i>	3
<i>Comandra umbellata</i>	0.45	0	<i>Oxalis stricta</i>	3
<i>Desmodium canadensis</i>	0.45	n/a	<i>Panicum implicatum</i>	3
<i>Elymus canadensis</i>	0.45	0	<i>Plantago rugellii</i>	3
<i>Equisetum arvense</i>	0.45	0	<i>Prunella vulgaris lanceolata</i>	3
<i>Galium asprellum</i>	0.45	0	<i>Quercus alba</i>	3
<i>Hackelia virginiana</i>	0.45	0	<i>Rubus occidentalis</i>	3
<i>Helianthus grosseserratus</i>	0.45	0	<i>Rudbeckia hirta</i>	3
<i>Juncus dudleyi</i>	0.45	0	<i>Solidago gigantea</i>	3
<i>Oxalis stricta</i>	0.45	0	<i>Taenidia integerrima</i>	3
<i>Panicum implicatum</i>	0.45	0	<i>Trillium recurvatum</i>	3
<i>Plantago rugellii</i>	0.45	0	<i>Erythronium albidum</i>	3
<i>Prunus virginiana</i>	0.45	n/a	<i>Allium cernuum</i>	3
<i>Prunella vulgaris lanceolata</i>	0.45	0	<i>Alliaria petiolata</i>	2
<i>Quercus alba</i>	0.45	0	<i>Amphicarpaea bracteata</i>	2
<i>Rubus occidentalis</i>	0.45	0	<i>Arisaema triphyllum</i>	2
<i>Rudbeckia hirta</i>	0.45	0	<i>Carex bebbii</i>	2
<i>Taenidia integerrima</i>	0.45	0	<i>Carex blanda</i>	2
<i>Trillium recurvatum</i>	0.45	0	<i>Carex lacustris</i>	2
<i>Erythronium albidum</i>	0.45	0	<i>Carya ovata</i>	2
<i>Allium cernuum</i>	0.45	0	<i>Carex stricta</i>	2
<i>Alliaria petiolata</i>	0.30	0	<i>Dactylis glomerata</i>	2
<i>Amphicarpaea bracteata</i>	0.30	0	<i>Eleocharis elliptica</i>	2
<i>Arisaema triphyllum</i>	0.30	0	<i>Erigeron annuus</i>	2

APPENDIX 1:
Continued.

Mean Plot Cover			Plot Frequency	
Taxon	mean	±s.e.m.	Taxon	freq
<i>Carex bebbii</i>	0.30	0	<i>Erigeron sp.</i>	2
<i>Carex blanda</i>	0.30	0	<i>Erigeron philadelphicus</i>	2
<i>Dactylis glomerata</i>	0.30	0	<i>Eupatorium rugosum</i>	2
<i>Erigeron annuus</i>	0.30	0	<i>Gentiana flavida</i>	2
<i>Erigeron sp.</i>	0.30	0	<i>Glechoma hederacea</i>	2
<i>Erigeron philadelphicus</i>	0.30	0	<i>Hydrophyllum virginianum</i>	2
<i>Eupatorium rugosum</i>	0.30	0	<i>Hypoxis hirsuta</i>	2
<i>Gentiana flavida</i>	0.30	0	<i>Hypericum punctatum</i>	2
<i>Glechoma hederacea</i>	0.30	0	<i>Lilium michiganense</i>	2
<i>Hydrophyllum virginianum</i>	0.30	0	<i>Onoclea sensibilis</i>	2
<i>Hypoxis hirsuta</i>	0.30	0	<i>Panicum latifolium</i>	2
<i>Hypericum punctatum</i>	0.30	0	<i>Poaceae</i>	2
<i>Lilium michiganense</i>	0.30	0	<i>Rhamnus frangula</i>	2
<i>Panicum latifolium</i>	0.30	0	<i>Silphium terebinthinaceum</i>	2
<i>Poaceae</i>	0.30	0	<i>Smilax lasioneura</i>	2
<i>Rhamnus frangula</i>	0.30	0	<i>Smilacina stellata</i>	2
<i>Smilax lasioneura</i>	0.30	0	<i>Solidago sp.</i>	2
<i>Smilacina stellata</i>	0.30	0	<i>Solidago rigida</i>	2
<i>Solidago sp.</i>	0.30	0	<i>Agastache nepetoides</i>	1
<i>Solidago rigida</i>	0.30	0	<i>Anemonella thalictroides</i>	1
<i>Agastache nepetoides</i>	0.15	n/a	<i>Arctium minus</i>	1
<i>Anemonella thalictroides</i>	0.15	n/a	<i>Asclepias exaltata</i>	1
<i>Arctium minus</i>	0.15	n/a	<i>Atriplex patula</i>	1
<i>Asclepias exaltata</i>	0.15	n/a	<i>Barbarea vulgaris</i>	1
<i>Atriplex patula</i>	0.15	n/a	<i>Carex buxbaumii</i>	1
<i>Barbarea vulgaris</i>	0.15	n/a	<i>Carex cephalophora</i>	1
<i>Carex buxbaumii</i>	0.15	n/a	<i>Carex tenera echinoides</i>	1
<i>Carex cephalophora</i>	0.15	n/a	<i>Carex tribuloides</i>	1
<i>Carex tenera echinoides</i>	0.15	n/a	<i>Cinna arundinacea</i>	1
<i>Carex tribuloides</i>	0.15	n/a	<i>Cirsium discolor</i>	1
<i>Cinna arundinacea</i>	0.15	n/a	<i>Convolvulus sepium</i>	1
<i>Cirsium discolor</i>	0.15	n/a	<i>Desmodium canadense</i>	1
<i>Convolvulus sepium</i>	0.15	n/a	<i>Dioscorea villosa</i>	1
<i>Dioscorea villosa</i>	0.15	n/a	<i>Dodecatheon meadia</i>	1
<i>Dodecatheon meadia</i>	0.15	n/a	<i>Eryngium yuccifolium</i>	1
<i>Eryngium yuccifolium</i>	0.15	n/a	<i>Gentiana andrewsii</i>	1
<i>Gentiana andrewsii</i>	0.15	n/a	<i>Geum laciniatum trichocarpum</i>	1
<i>Geum laciniatum trichocarpum</i>	0.15	n/a	<i>Heuchera richardsonii</i>	1
<i>Heuchera richardsonii</i>	0.15	n/a	<i>Lonicera tatarica</i>	1
<i>Lonicera tatarica</i>	0.15	n/a	<i>Luzula multiflora</i>	1
<i>Luzula multiflora</i>	0.15	n/a	<i>Mentha arvensis</i>	1
<i>Mentha arvensis</i>	0.15	n/a	<i>Oxalis europea</i>	1
<i>Oxalis europea</i>	0.15	n/a	<i>Parthenium integrifolium</i>	1
<i>Parthenium integrifolium</i>	0.15	n/a	<i>Penstemon digitalis</i>	1
<i>Penstemon digitalis</i>	0.15	n/a	<i>Polygonum punctatum</i>	1
<i>Polygonum punctatum</i>	0.15	n/a	<i>Prunus virginiana</i>	1
<i>Quercus sp.</i>	0.15	n/a	<i>Quercus sp.</i>	1
<i>Ranunculus abortivus</i>	0.15	n/a	<i>Ranunculus abortivus</i>	1
<i>Rosa arkansana suffulta</i>	0.15	n/a	<i>Rosa arkansana suffulta</i>	1
<i>Rosa blanda</i>	0.15	n/a	<i>Rosa blanda</i>	1

APPENDIX 1:
Continued.

Mean Plot Cover			Plot Frequency	
Taxon	mean	±s.e.m.	Taxon	freq
<i>Rubus allegheniensis</i>	0.15	n/a	<i>Rubus allegheniensis</i>	1
<i>Rubus sp.</i>	0.15	n/a	<i>Rubus sp.</i>	1
<i>Rudbeckia subtomentosa</i>	0.15	n/a	<i>Rudbeckia subtomentosa</i>	1
<i>Rumex crispus</i>	0.15	n/a	<i>Rumex crispus</i>	1
<i>Salix discolor</i>	0.15	n/a	<i>Salix discolor</i>	1
<i>Sanicula gregaria</i>	0.15	n/a	<i>Sanicula gregaria</i>	1
<i>Silene stellata</i>	0.15	n/a	<i>Silene stellata</i>	1
<i>Smilax tamnoides hispida</i>	0.15	n/a	<i>Smilax tamnoides hispida</i>	1
<i>Solanum dulcamara</i>	0.15	n/a	<i>Solanum dulcamara</i>	1
<i>Spartina pectinata</i>	0.15	n/a	<i>Spartina pectinata</i>	1
<i>Trifolium pratense</i>	0.15	n/a	<i>Trifolium pratense</i>	1
<i>Vicia americana</i>	0.15	n/a	<i>Vicia americana</i>	1
<i>Vitis riparia</i>	0.15	n/a	<i>Vitis riparia</i>	1
<i>Lobelia siphilitica</i>	0.15	n/a	<i>Lobelia siphilitica</i>	1
<i>Solidago graminifolia</i>	0.15	n/a	<i>Solidago graminifolia</i>	1

APPENDIX 2:

Distribution of ground layer species frequencies across light gradient as measured by percent canopy openness. For each species, bordered area indicates decile of canopy openness which holds median value. Shaded area represents range in light gradient in which species was recorded. Species names in bold are characteristic savanna species (refer to Table 8). Columns on right represent total frequency out of 50 plots and growth form (f = forb, g = graminoid, t = tree, s = shrub, v = vine).

Decile	Sun ←-----→ Shade										Total Freq	Form
	1	2	3	4	5	6	7	8	9	10		
<i>Carex buxbaumii</i>	1										1	g
<i>Desmodium canadensis</i>	1										1	f
<i>Eleocharis elliptica</i>	2										2	g
<i>Eryngium yuccifolium</i>	1										1	f
<i>Hypoxis hirsuta</i>	2										2	f
<i>Parthenium integrifolium</i>	1										1	f
<i>Rudbeckia subtomentosa</i>	1										1	f
<i>Silphium terebinthinaceum</i>	2										2	f
<i>Carex lacustris</i>	1	1									2	g
<i>Juncus dudleyi</i>	2	1									3	g
<i>Onoclea sensibilis</i>	1	1									2	f
<i>Galium obtusum</i>	3	1	1								5	f
<i>Equisetum arvensis</i>	2			1							3	g
<i>Helianthus grosseserratus</i>	2			1							3	f
<i>Amphicarpaea bracteata</i>	1		1								2	v
<i>Calamagrostis canadensis</i>	2	2	2		1						7	g
<i>Solidago gigantea</i>	1	1						1			3	f
<i>Senecio aureus</i>	2	1						1		1	5	f
<i>Convolvulus sepium</i>		1									1	f
<i>Heuchera richardsonii</i>		1									1	f
<i>Mentha arvensis</i>		1									1	f
<i>Salix discolor</i>		1									1	t
<i>Spartina pectinata</i>		1									1	g
<i>Carex pellita</i>		2								1	3	g
<i>Coreopsis tripteris</i>	2		2	1	1						6	f
<i>Lycopus americanus</i>	1	1		1	1						4	f
<i>Lilium michiganense</i>	1					1					2	f
<i>Stachys tenuis hispida</i>	1	1	3		1					1	7	f
<i>Carex blanda</i>			2								2	g
<i>Geum laciniatum tricho.</i>			1								1	f
<i>Rosa blanda</i>			1								1	s
<i>Carex stricta</i>			1	1							2	g
<i>Trillium recurvatum</i>			2		1						3	f
<i>Elymus canadensis</i>			2			1					3	g
<i>Pycnanthemum virginianum</i>	2	1		2	1		1				7	f
<i>Veronicastrum virginicum</i>	4	2	2	4	3	1	1	2		2	21	f
<i>Rubus pensilvanicus</i>	1	1	1	2	2			1	1	1	10	s
<i>Agrostis alba</i>	1	2	2	2	2	1	1	1		1	13	g
<i>Comandra umbellata</i>		1		1	1						3	f
<i>Smilacina stellata</i>		1					1				2	f
<i>Panicum implicatum</i>		1		1				1			3	g
<i>Monarda fistulosa</i>		1		1				1			3	f
<i>Arenaria lateriflora</i>		1		2				1		1	5	f
<i>Zizia aurea</i>		2	1	2	1				2	1	9	f
<i>Erigeron annuus</i>			1		1						2	f
<i>Quercus sp.</i>				1							1	t

APPENDIX 2:
Continued.

Decile	Sun ←-----→ Shade										Total Freq	Form	
	1	2	3	4	5	6	7	8	9	10			
<i>Silene stellata</i>				1								1	f
<i>Smilax tannoides hispida</i>				1								1	f
<i>Phalaris arundinacea</i>	1	2		1	1	2			2			9	g
<i>Aster simplex</i>	3	3	2	3	3	3	2	2	1	1		23	f
<i>Carex tenera</i>	2	3			1	1		2	1	1		11	g
<i>Cornus racemosa</i>	3	2	2	3	5	2	1		2	1		21	s
<i>Oxalis</i> sp.	2			1	2	1	1	1		1		9	f
<i>Oxypolis rigidior</i>	1		1	2		1		1		2		8	f
<i>Poa pratensis</i>	1	2	2	1	2	1	1	1	3	2		16	g
<i>Rubus occidentalis</i>	1				1					1		3	s
<i>Smilax</i> sp.	1	3	3	3	3	4	2	2	1	3		25	f
<i>Solidago altissima</i>	1	4	3	3	4	4	2	3	3	3		30	f
<i>Sphenopholis intermedia</i>	2	2	1	2	4	1	1	2		1		16	g
<i>Tradescantia ohiensis</i>	1	3	2	3	3	1	3	2	2	3		23	f
<i>Fraxinus</i> sp.		1		1	1	1			1			5	t
<i>Hypericum punctatum</i>		1							1			2	f
<i>Viola sororia</i>		2	1	2	1	2	1	1	1			11	f
<i>Allium canadensis</i>		1	1		1	1			1	1		6	f
<i>Helianthus divaricatus</i>		1	5	4	1	1	2	1	4	2		21	f
<i>Rhamnus cathartica</i>		3	2	2	3	3	2	1	2	2		20	s
<i>Solidago rigida</i>			1				1					2	f
<i>Corylus americana</i>			1		2				1	1		5	s
<i>Daucus carota</i>			2	1	1	1		1		1		7	f
<i>Carex molesta</i>				1	1	1						3	g
<i>Prenanthes alba</i>				1	2					1		4	f
<i>Anemonella thalictroides</i>					1							1	f
<i>Barbarea vulgaris</i>					1							1	s
<i>Dioscorea villosa</i>					1							1	v
<i>Glechoma hederacea</i>					2							2	f
<i>Penstemon digitalis</i>					1							1	f
<i>Trifolium pratense</i>					1							1	f
<i>Vicia americana</i>					1							1	f
<i>Fragaria virginiana</i>	1	1	3	1	4	3	2	2	3	2		22	f
<i>Rosa carolina</i>	1	1	1	2	5	3	3	2	1	2		21	s
<i>Solidago juncea</i>	1	1	1	3	1	1	3	2	2	1		16	f
<i>Taraxacum officinale</i>	1	1	3	3	2	5	4	2	5	4		30	f
<i>Oxalis stricta</i>		1				2						3	f
<i>Circaea lutetiana canadensis</i>		1	1		1	3	3	1	1			11	f
<i>Bidens</i> sp.		1		1	1	2			3	1		9	f
<i>Cirsium arvense</i>		2			2	2		1	2	1		10	f
<i>Geranium maculatum</i>		2	1	3	1	2	3	1	1	1		15	f
<i>Rhamnus frangula</i>		1								1		2	s
<i>Erigeron philadelphicus</i>			1						1			2	f
<i>Poa compressa</i>			1	2	1	2	2	2	1			11	g
<i>Festuca elatior</i>			2	1			2			1		6	g
<i>Galium asprellum</i>				1		1	1					3	f
<i>Carex bebbii</i>				1				1				2	g
<i>Hystrix patula</i>				1	1	1	1		1	1		6	g
<i>Juncus tenuis</i>				1	1			1		1		4	g
<i>Aster praealtus</i>				1	1	2		1	1	1		7	f

APPENDIX 2:
Continued.

Decile	Sun ←-----→ Shade										Total Freq	Form	
	1	2	3	4	5	6	7	8	9	10			
<i>Elymus virginicus</i>					1	2	2					5	g
<i>Rudbeckia hirta</i>					1	1	1					3	f
<i>Smilax lasioneura</i>					1		1					2	f
<i>Thalictrum dasycarpum</i>					1	2	1					4	f
<i>Erigeron</i> sp.					1			1				2	f
<i>Gentiana flavida</i>					1			1				2	f
<i>Solidago</i> sp.					1			1				2	f
<i>Cinna arundinacea</i>						1						1	g
<i>Eupatorium rugosum</i>						1	1					2	f
<i>Arisaema triphyllum</i>						1	1					2	f
<i>Carex</i> sp.	1						1		1	1		4	g
<i>Agrimonia gryposepala</i>		1	2	1		1	2	2	2			11	f
<i>Phleum pratense</i>		1	1			1	2	1	1			7	g
<i>Ranunculus septentrionalis</i>		2		1						1		4	f
<i>Potentilla simplex</i>		1	2	1	1	5	5	3	4	4		26	f
<i>Aster lateriflorus</i>		1	2	1	1	2	4	2	3	3		19	f
<i>Carex pensylvanica</i>			2			1	3	2				8	g
<i>Aster saggitifolius</i>			2				2		2			6	f
<i>Anemone quinquefolia</i>			1			3	2		3	1		10	f
<i>Taenidia integerrima</i>				1			2					3	f
<i>Aquilegia canadensis</i>				1			1		1			3	f
<i>Erythronium albidum</i>				1			1		1			3	f
<i>Achillea millefolium</i>					1		2					3	f
<i>Sanicula marilandica</i>				1	1		1		1	1		5	f
<i>Cerastium vulgatum</i>					1		1	1				3	f
<i>Alliaria petiolata</i>					1				1			2	f
<i>Quercus alba</i>					1		1		1			3	t
<i>Prunella vulgaris lanceolata</i>						1	1			1		3	f
<i>Carex tenera echinoides</i>							1					1	g
<i>Lonicera tatarica</i>							1					1	s
<i>Luzula multiflora</i>							1					1	g
<i>Dactylis glomerata</i>							1	1				2	g
<i>Panicum latifolium</i>							1		1			2	g
<i>Carex normalis</i>	1				2		1		3	1		8	g
<i>Aster novaeangliae</i>			1	1	1							3	f
<i>Smilacina racemosa</i>				1		1	1		2	1		6	f
<i>Solidago ulmifolia</i>					1	1		1	1	1		5	f
<i>Geum canadensis</i>					1	1	1	2		3		8	f
<i>Aster</i> sp.							1	1	1			3	f
<i>Allium cernuum</i>							1			1		3	f
<i>Lobelia siphilitica</i>								1				1	f
<i>Oxalis europea</i>								1				1	f
<i>Polygonum punctatum</i>								1				1	f
<i>Cirsium discolor</i>								1				1	f
<i>Gentiana andrewsii</i>								1				1	f
<i>Atriplex patula</i>								1				1	f
<i>Agastache nepetoides</i>								1				1	f
<i>Carya ovata</i>								1	1			2	t
<i>Hackelia virginiana</i>								2	1			3	f

APPENDIX 2:
Continued.

Decile	Sun ←-----→ Shade										Total Freq	Form	
	1	2	3	4	5	6	7	8	9	10			
<i>Arctium minus</i>									1			1	f
<i>Asclepias exaltata</i>									1			1	f
<i>Carex cephalophora</i>									1			1	g
<i>Dodecatheon meadia</i>									1			1	f
<i>Ranunculus abortivus</i>									1			1	f
<i>Rubus</i> sp.									1			1	s
<i>Solanum dulcamara</i>									1			1	f
<i>Vitis riparia</i>									1			1	v
<i>Hydrophyllum virginianum</i>									1	1		2	f
Poaceae									1	1		2	g
<i>Plantago rugellii</i>								1		2		3	f
<i>Carex tribuloides</i>										1		1	g
<i>Prunus virginiana</i>										1		1	s
<i>Rosa arkansana suffulta</i>										1		1	s
<i>Rubus allegheniensis</i>										1		1	s
<i>Rumex crispus</i>										1		1	f
<i>Sanicula gregaria</i>										1		1	f
<i>Solidago graminifolia</i>										1		1	f

VEGETATION SURVEY OF TOMLIN TIMBER NATURE PRESERVE, MASON COUNTY, ILLINOIS

Loy R. Phillippe¹, James Ellis¹, Daniel T. Busemeyer²,
William E. McClain³, and John E. Ebinger⁴

ABSTRACT: Tomlin Timber Nature Preserve is a dry to dry-mesic sand forest. When surveyed by the Illinois Natural Areas Inventory in 1976, the overstory was dominated by *Quercus velutina* (black oak). *Sassafras albidum* (sassafras) was second in importance, dominated the woody seedling and sapling layer, and was common in the small tree diameter classes. In 2004, 28 years after the initial survey, *Sassafras albidum* dominated the overstory with an importance value (IV) of 54.9 (possible 200), an average dbh of 24.4 cm, and with most individuals in the 10–40 cm diameter classes. *Quercus velutina*, in contrast, was second with an IV of 38.5, an average dbh of 62.7, and dominated the larger diameter classes. Dead-standing and dead-downed black oaks were common and averaged 51.7 stems/ha. The change in dominance appears to be due to a combination of natural mortality and oak wilt which was common in the preserve in the early 1980s. A total of 157 vascular plant taxa were documents from the 8-ha preserve.

INTRODUCTION

Wind-blown sand deposits, which account for nearly 5% of the land surface of Illinois, occur on glacial outwash plains associated with erosional events of Wisconsin Glaciation in the northern half of the state (Schwegman 1973, King 1981). The Illinois River sand deposits of Cass and Mason counties in the central part of the state were formed about 14,500 years ago when glacial moraines were breached, resulting in the Kankakee Torrent (Willman and Frye 1970). These flood waters carried huge amounts of sand and gravel that were deposited when the waters slowed upon entering the broad lowlands of the Illinois River valley below present day Hennepin. Many high quality natural areas that are now Illinois Nature Preserves occur on these sand deposits. We are studying these preserves to determine the composition and structure of the plant communities of these sand deposits.

The early works of Hart and Gleason (1907) and Gleason (1910) were the first extensive studies of the sand area vegetation of the state. A few other studies were completed prior to the early 1990s, and consisted of plant species lists for a few natural areas (Maier 1976, Schwegman 1977). More recently, the structure and composition of some upland dry sand forest communities and dry sand savanna communities were examined (Jenkins et al. 1991, Coates et al. 1992, McClain et al. 2002). The purpose of the present study was to examine the composition and structure of Tomlin Timber Nature Preserve, a sand forest remnant on the Illinois River sand deposits in Mason County.

METHODS

Site Description

Dedicated as a nature preserve in 1987, Tomlin Timber is located about 3 km south of Easton, Mason County, Illinois (40.2009°N, 89.859°W, WGS84/NAD83; NE1/4 SW1/4 S11 T20N R7W). The preserve is on a series of low dunes that lie between 158 and 165 m above sea level in the Illinois River Section of the Mississippi River and Illinois Rivers Sand Areas Natural Division (Schwegman 1973). The soils are excessively drained Bloomfield sand (Calsyn 1995); part of the dune and swale topography known as the Parkland Formation (Willman and Frye 1970).

¹ Illinois Natural History Survey, Champaign, Illinois 61820.

² Ghostpine Environmental Services Ltd., Calgary, Alberta.

³ Illinois State Museum, Springfield, Illinois 62706.

⁴ Emeritus Professor, Dept. of Biological Sciences, Eastern Illinois University, Charleston, Illinois 61920
author for correspondence.

Little is known about the past history of this 8-ha tract of timber. A comment by Onstot (1902) mentions that Walker's Grove (of which Tomlin Timber is a remnant) "embraces 40 acres of as fine a body of timber as can be found anywhere; a fine growth of oaks, black walnut, soft and sugar maple, hickory, butternut, mulberry, sassafras, redbud, pawpaw, and dogwood". The size of the oaks, most of which are in the 50–70 cm diameter classes, suggests that Walker's Grove was never clear-cut. When purchased by the Tomlin family in 1912 a one-room schoolhouse was located on the east edge of the property. When surveyed by the Illinois Natural Areas Inventory (White 1978), the owner indicated that the woods had been selectively logged 50 to 60 years ago, but never grazed. Don McFall (Illinois Department of Natural Resources, personal communication) mentions that he first walked through the woods in the early 1980s, and there was a fairly dense woody understory and a number of large dead black oaks.

Based on weather data from Havana about 21 km to the northwest, mean annual precipitation is 96.0 cm, with May having the highest rainfall (11.3 cm). Mean annual temperature is 10.8°C with the hottest month being July (average of 24.6°C), and the coldest January (average of –5.0°C). Frost-free days range from 140 to 206, with the average being 173 days per year (www.sws.uiuc.edu 2007).

Data

During the growing seasons of 2003 and 2004 the study site was visited 12 times. A representative of every vascular plant species was collected, their habitat recorded, and voucher specimens deposited in the herbarium of the Illinois Natural History Survey, Champaign, Illinois (ILLS). Criteria for designating non-native species follows Mohlenbrock (2002) and Gleason and Cronquist (1991). Nomenclature follows Mohlenbrock (2002). All species are listed in Appendix I along with the collector and collecting number.

During late summer of 2004, a 150 m by 300 m section of the natural area was surveyed by dividing the area into 72 contiguous quadrats 25 m × 25 m, for a total of 4.5 ha.). All living and dead-standing woody individuals ≤10.0 cm dbh (diameter at breast height where breast height is 1.4 m above the ground) were identified and diameters recorded. From this data, living-stem density (stems/ha), basal area (m²/ha), relative density, relative dominance, importance value (IV), and average diameter (cm) were calculated for each species. Determination of the IV follows the procedure used by McIntosh (1957), and is the sum of the relative density and relative dominance (basal area). Dead-standing density (stem/ha) and basal area (m²/ha) was also determined.

Woody understory composition and density (stems/ha) was determined using nested circular plots 0.0001, 0.001, and 0.01 ha in size located at 15 m intervals along randomly located east–west transects within the study area (72 plots). Four additional 0.0001 ha circular plots were located 7 m from the center points of each of the 72 plot centers along cardinal compass directions (360 plots). In the 0.0001 ha plots, woody seedlings (≤50 cm tall) were counted; in the 0.001 ha circular plots small saplings (>50 cm tall and <2.5 cm dbh) were recorded; and in the 0.01 ha circular plots large saplings (2.5–9.9 cm dbh) were tallied.

RESULTS

At Tomlin Timber Nature Preserve a total of 157 vascular plant species within 125 genera and 61 families were documented. Of these, three were fern and fern-allies, one was a gymnosperm, 122 were dicots in 98 genera and 50 families, and 31 were monocots in 23 genera and seven families. No threatened or endangered species were found. The predominant plant families were the Poaceae and Asteraceae with 17 taxa each. Thirty one exotic plant taxa were found, representing about 19% of the flora of the preserve (Appendix I).

Nineteen woody species were present in the overstory (Table 1). *Sassafras albidum* (sassafras) dominated the smaller diameter classes with most individuals being less than 40 cm dbh. This species had an IV of 54.9, averaged 132.5 stems/ha, and 24.4 cm dbh. *Quercus velutina* (black oak), restricted to the larger diameter classes, was second in IV (38.5), averaged 25.4 stems/ha, and 62.7 cm dbh. The remaining trees were mostly in the 10–39 cm diameter classes, and included *Carya texana* (black hickory) which averaged 90.1 stems/ha, *Celtis occidentalis* (hackberry), 80.7 stems/ha, and *Prunus serotina* (black cherry), 52.8 stems/ha, all with IVs below 31 and average diameters less than 20 cm dbh.

The woody understory was dense with 18,639 woody seedlings/ha, 4,862 small saplings/ha, and 1,222 large saplings/ha (Table 2). Few open areas existed in the woody understory, the more open areas being under the extensive colonies of *Asimina triloba* (pawpaw). *Asimina triloba* averaged 4,028 seedlings/ha, 2,986 small saplings/ha, 854 large saplings/ha, along with 14.9 stems/ha that exceeded 10 cm dbh (Tables 1 and 2). *Celtis occidentalis*, *Sassafras albidum*, *Carya cordiformis* (bitternut hickory), and *Ulmus americana* (American elm) were also extremely common. Many other tree species were present, but in relatively low numbers. Woody shrubs and vines were also important in the understory, *Toxicodendron radicans* (poison ivy), *Rubus pensilvanicus* (blackberry), and *Ribes missouriense* (Missouri gooseberry) being the most common (Table 2).

Dead-standing individuals averaged 43.5 stems/ha with a basal area of 5.059 m²/ha, the most important being *Quercus velutina*, *Sassafras albidum*, and *Ulmus americana* (Table 3). *Sassafras albidum* exceeded *Q. velutina* in the number of dead-standing stems/ha, but dead-standing *Q. velutina* was responsible for most of the basal area (4.188 of 5.059 m²/ha). Dead-downed trees were common and averaged 46.7 stems/ha with a basal area of 6.115 m²/ha. *Quercus velutina* was the most important taxon in this category accounting for 37.3 stems/ha and 5.781 m²/ha of basal area (Table 3).

DISCUSSION

Using Government Land Office (GLO) survey records, Rodgers and Anderson (1979) described the pre-settlement vegetation of Mason County. They found that *Quercus velutina* was the dominant woody species in open forest communities where it usually accounted for half of the IV. Species diversity was high in these open forests with *Carya* spp. (hickories), *Acer* spp. (maples), *Quercus alba* (white oak), *Ulmus* spp. (elms), and *Fraxinus* spp. (ash) following *Q. velutina* in IV. The presence of many small diameter witness trees reported in the GLO survey indicates that oaks and hickories were reproducing, and these relatively shade-intolerant species were replacing themselves (Rodgers and Anderson 1979).

Tomlin Timber is very different today compared to the early 1800s due to a reduced fire frequency followed by a total absence of fire in recent decades (Taft 1997). Frequent fires in pre-settlement times were probably responsible for maintaining a relatively open forest with a reduced understory (Ebinger and McClain 1991, McClain and Elzinga 1994). Thick bark and the ability to reproduce by sprouts gave oaks a competitive advantage in areas of high fire frequencies. Fire frequency and intensity dictated oak density in this pre-settlement landscape (Anderson 1991, Abrams 1992). The compositional stability of these open forest communities indicates that the open habitat necessary for the reproduction of these species was being maintained, probably by fire.

When surveyed by the Illinois Natural Areas Inventory in 1976, the preserve was considered an old-growth "grade A" dry upland sand forest due to the "excellent timber of good size, height, and form" (Wallace and Rowe 1976). Tree density averaged 244 stems/ha with a basal area of 27.6 m²/ha. *Quercus velutina* was the dominant overstory species with 120 stems/ha and a basal area of 22.0 m²/ha, most of the individuals in the 50 to 70 cm diameter classes. *Sassafras albidum*, *Carya tomentosa* (mockernut hickory), and black hickory followed in importance. The sapling layer averaged 3,900 stems/ha, *Sassafras*

albidum being the dominant species with 1,700 stems/ha (Wallace and Rowe 1976).

Most of the forests previously studied in the Illinois River sand deposits were closed canopy dry sand forests located on dune deposits where *Quercus velutina* and *Q. marilandica* (blackjack oak) were usually the leading dominants along with a few hickory species. *Carya texana* occasionally replaced *Q. marilandica* as second in IV in those forests, while *Sassafras albidum* and *Ulmus americana* were not present. These forests probably represent sand savannas that have since become closed forests due to fire suppression (Jenkins et al. 1991, Coates et al. 1992, McClain et al. 2002).

Tomlin Timber was probably an open, dry-mesic sand forest (woodland) community in pre-settlement times. Canopy closure and the increased importance of mesic trees resulting from fire suppression, has altered the structure of Tomlin Timber. With canopy closure shade-intolerant *Quercus velutina* could not effectively reproduce. *Sassafras albidum*, a fire-sensitive, but relatively shade-tolerant species, became the dominant understory species, eventually entered the canopy and now is the dominant species.

The high mortality of *Quercus velutina* observed in the woods indicates that this species was susceptible to oak wilt (Henry et al. 1944). Oak wilt disease was observed in the woods in the early 1980s, and several large diameter black oaks were killed (W.E. McClain, personal observation). The death of large oaks created canopy openings that were filled by *Sassafras albidum*. Though the growth of *S. albidum* is not rapid, this species has a relatively high gap-phase-replacement potential (please explain this term) and commonly reproduces by root suckers.

During the present survey no *Quercus velutina* sapling or 10–20 cm diameter class trees were observed suggesting that this species will continue to decrease in importance as the veteran trees die. Also, few individuals of *Q. velutina* were in the 20–29 cm diameter class. Tomlin timber is another example of oaks being replaced by more mesic tree species due to a reduced fire frequency (Ebinger and McClain 1991, Taft 1977). The loss of dominance by *Q. velutina* since the 1976 inventory has been profound. This site no longer qualifies as an "old growth grade A" forest community.

LITERATURE CITED

- Abrams, M. D. 1992. Fire and the development of oak forests. *BioScience* 42:346–353.
- Anderson, R. C. 1991. Presettlement forest of Illinois. Pages 9–19. in G. V. Burger, J. E. Ebinger, and G. S. Wilhelm (editors). *Proceedings of the Oak Woods*

- Management Workshop. Eastern Illinois University, Charleston, Illinois.
- Calsyn, D. E. 1995. Soil survey of Mason County, Illinois. Soil Report 146, University of Illinois Agricultural Experiment Station, Urbana. 211 pp.
- Coates, D. T., S. E. Jenkins, J. E. Ebinger, and W. E. McClain. 1992. Woody vegetation survey of Barkhausen Woods, a closed canopy sand forest in Mason County, Illinois. *Erigenia* 12:1–6.
- Ebinger, J. E. and W. E. McClain. 1991. Forest succession in the prairie peninsula of Illinois. *Illinois Natural History Survey Bulletin* 34:375–381.
- Gleason, H. A. 1910. The vegetation of the inland sand deposits of Illinois. *Bulletin of the Illinois State Laboratory of Natural History* 9:21–174.
- Gleason, H. A. and A. Cronquist. 1991. *Manual of vascular plants of northeastern United States and adjacent Canada*. 2nd edition. The New York Botanical Garden, Bronx, New York.
- Hart, C. A. and H. A. Gleason. 1907. On the biology of the sand areas of Illinois. *Bulletin of the Illinois State Laboratory of Natural History* 7:137–272.
- Henry, B. W., C. S. Moses, C. A. Richards, and A. J. Riker. 1944. Oak wilt, its significance, symptoms, and cause. *Phytopathology* 34:636–645.
- Jenkins, S. E., J. E. Ebinger, and W. E. McClain. 1991. Woody vegetation survey of Bishop's Woods, a sand forest in Mason County, Illinois. *Transactions of the Illinois State Academy of Science* 84:20–27.
- King, J. E. 1981. Late Quaternary vegetational history of Illinois. *Ecological Monographs* 51:43–62.
- Maier, C. T. 1976. An annotated list of the vascular plants of Sand Ridge State Forest, Mason County, Illinois. *Transactions of the Illinois State Academy of Science* 69:153–175.
- McClain, W. E. and S. L. Elzinga. 1994. The occurrence of prairie and forest fires in Illinois and other Midwestern states, 1679 to 1854. *Erigenia* 13:79–90.
- McClain, W. E., S. D. Turner, and J. E. Ebinger. 2002. Vegetation of forest communities at the Sand Prairie-Scrub Oak Nature Preserve, Mason County, Illinois. *Transactions of the Illinois State Academy of Science*. 95:37–46.
- McIntosh, R. P. 1957. The York Woods. A case history of forest succession in southern Wisconsin. *Ecology* 38:29–37.
- Mohlenbrock, R. H. 2002. *Vascular Flora of Illinois*. Southern Illinois University Press, Carbondale and Edwardsville. x+490 pp.
- Onstot, T. G. 1902. *Pioneers of Menard and Mason counties*. Published by the author, Forestry City, Illinois: 400 pp.
- Rodgers, C. S. and R. C. Anderson. 1979. Presettlement vegetation of two prairie peninsula counties. *Botanical Gazette* 140:232–240.
- Schwegman, J. E. 1973. Comprehensive plan for the Illinois nature preserves system. Part 2. The natural divisions of Illinois. Illinois Nature Preserves Commission, Rockford, Illinois.
- Schwegman, J. E. 1977. An annotated list of the flowering plants of Sand Prairie-Scrub Oak Nature Preserve. Unpublished report submitted to the Illinois Department of Conservation, Springfield, Illinois map+26 pp.
- Taft, J. B. 1997. Savanna and open woodland communities. Pages 24–54. *in* M. W. Schwartz (editor). *Conservation in highly fragmented landscapes*. Chapman and Hall, New York.
- Wallace, D. and E. Rowe. 1976. Mattson Woods. Illinois Natural Areas Inventory final field survey form. Unpublished report on file at the Illinois Department of Natural Resources, Springfield, Illinois.
- White, J. 1978. Illinois Natural Areas Inventory. Technical report. Volume I. Survey methods and results. Illinois Natural Areas Inventory, Urbana. xix+426 pp.
- Willman, H. B. and J. C. Frye. 1970. Pleistocene Stratigraphy of Illinois. *Illinois State Geological Survey Bulletin* 94:1–204.
- www.sws.uiuc.edu. 2007. Records for Havana, Illinois. The Weather Channel.

Table 1: Density by diameter class (stems/ha), basal area (m²/ha), relative density, relative dominance, importance value, and average diameter for the woody species at Tomlin Timber Nature Preserve, Mason County, Illinois.

Species	Diameter Classes (cm)					Total #/ha	Basal Area m ² /ha	Rel. Den.	Rel. Dom.	I.V.	Av. Diam. (cm)
	10–19	20–29	30–39	40–49	50+						
<i>Sassafras albidum</i>	41.1	59.8	26.7	4.2	0.7	132.5	6.898	26.5	28.4	54.9	24.4
<i>Quercus velutina</i>	–	0.7	0.9	1.1	22.7	25.4	8.102	5.1	33.4	38.5	62.7
<i>Carya texana</i>	51.6	34.0	3.8	0.7	–	90.1	2.905	18.1	12.0	30.1	19.3
<i>Celtis occidentalis</i>	64.7	13.1	2.0	0.7	0.2	80.7	1.900	16.2	7.8	24.0	16.2
<i>Prunus serotina</i>	42.0	8.0	2.2	0.4	0.2	52.8	1.380	10.6	5.7	16.3	16.7
<i>Ulmus americana</i>	31.8	5.8	–	–	–	37.6	0.791	7.5	3.3	10.8	15.7
<i>Carya tomentosa</i>	13.3	10.0	3.6	0.2	–	27.1	1.051	5.4	4.3	9.7	20.9
<i>Ulmus rubra</i>	24.4	4.4	0.4	–	–	29.2	0.626	5.9	2.6	8.5	15.7
<i>Asimina triloba</i>	14.9	–	–	–	–	14.9	0.166	3.0	0.7	3.7	11.8
Others ¹	4.2	1.3	1.1	0.9	0.4	7.9	0.466	1.7	1.8	3.5	–
Totals	288.0	137.1	40.7	8.2	24.2	498.2	24.285	100.0	100.0	200.0	

¹Includes *Juglans nigra* (black walnut), *Carya cordiformis* (bitternut hickory), *Morus rubra* (red mulberry), *Morus alba* (white mulberry), *Acer saccharum* (sugar maple), *Robinia pseudoacacia* (black locust), *Catalpa bignonioides* (catalpa), *Acer saccharinum* (silver maple), *Maclura pomifera* (Osage orange), and *Diospyros virginiana* (persimmon).

Table 2: Density (stems/ha) of woody understory species at Tomlin Timber Nature Preserve, Mason County, Illinois.

Species	Seedlings	Small Saplings	Large Saplings
<i>Asimina triloba</i>	4028	2986	854
<i>Celtis occidentalis</i>	2000	944	115
<i>Sassafras albidum</i>	1806	625	103
<i>Carya cordiformis</i>	1667	167	25
<i>Ulmus americana</i>	1222	56	18
<i>Ulmus rubra</i>	361	42	21
<i>Quercus velutina</i>	333	–	–
<i>Carya texana</i>	250	–	8
<i>Maclura pomifera</i>	139	–	11
<i>Morus alba</i>	111	28	–
<i>Prunus serotina</i>	83	14	61
<i>Gleditsia triacanthos</i>	28	–	–
<i>Juglans nigra</i>	–	–	4
<i>Acer negundo</i>	–	–	1
<i>Morus rubra</i>	–	–	1
<i>Toxicodendron radicans</i>	2194	–	–
<i>Rubus pensilvanicus</i>	1944	–	–
<i>Ribes missouriense</i>	1306	–	–
<i>Sambucus canadensis</i>	389	–	–
<i>Rubus occidentalis</i>	278	–	–
<i>Zanthoxylum americanum</i>	250	–	–
<i>Rubus flagellaris</i>	139	–	–
<i>Rosa multiflora</i>	83	–	–
<i>Lonicera maackii</i>	28	–	–
Totals	18639	4862	1222

Table 3: Density (stems/ha), basal area (m²/ha), and average diameter of the dead-standing and dead-downed tree species at Tomlin Timber Nature Preserve, Mason County, Illinois.

Tree Species	DEAD-STANDING			DEAD-DOWNED		
	Density (stems/ha)	Basal Area (m ² /ha)	Average Diameter (cm)	Density (stems/ha)	Basal Area (m ² /ha)	Average Diameter (cm)
<i>Quercus velutina</i>	14.4	4.188	59.2	37.3	5.781	43.1
<i>Sassafras albidum</i>	17.1	0.532	19.2	3.6	0.158	23.0
<i>Ulmus rubra</i>	4.2	0.083	15.5	2.9	0.079	18.3
<i>Ulmus americana</i>	2.7	0.085	19.3	1.8	0.059	20.0
<i>Prunus serotina</i>	2.0	0.057	17.7	0.2	0.010	23.8
<i>Carya tomentosa</i>	0.9	0.055	26.0	–	–	–
<i>Carya texana</i>	0.9	0.033	21.1	0.9	0.028	19.0
<i>Asimina triloba</i>	0.9	0.011	12.6	–	–	–
<i>Acer saccharinum</i>	0.4	0.015	20.8	–	–	–
Totals	43.5	5.059		46.7	6.115	

APPENDIX

Vascular species encountered at Tomlin Timber Nature Preserve, Mason County, Illinois, listed alphabetically by family under major plant groups. An asterisk indicates non-native (exotic) species (*). Following the scientific name, collecting numbers are given, preceded by the name of the collector, abbreviated as E for James Ellis and P Loy R. Phillippe.

PTERIDOPHYTES**DRYOPTERIDACEAE**

Dryopteris carthusiana (Villars) H. P. Fuchs, P 36729

ONOCLEACEAE

Onoclea sensibilis L., P36064

OPHIOGLOSSACEAE

Botrychium virginianum (L.) Sw., P36680

GYMNOSPERMS**CUPRESSACEAE**

Juniperus virginiana L., P36049

DICOTYLEDONEAE**ACANTHACEAE**

Ruellia humilis Nutt., P 35978

ACERACEAE

Acer negundo L., P 37298

Acer saccharinum L., P37360

Acer saccharum Marsh., P 37356

ANACARDIACEAE

Toxicodendron radicans (L.) Kuntze, P 36003

ANNONACEAE

Asimina triloba (L.) Dunal, P 36016

APIACEAE

Chaerophyllum procumbens (L.) Crantz, P 36674

Osmorhiza longistylis (Torr.) DC., P 36672.2

Sanicula canadensis L., P 36011

Sanicula odorata (Raf.) Pryer & Phillippe, P 36021

ASTERACEAE

Ageratina altissima (L.) R.M. King & H. Rob., P 36010

Ambrosia artemisiifolia L., P36036

Ambrosia trifida L., P36047

Arnoglossum atriplicifolia (L.) H. Rob., P 35972

Aster ontarionis Wieg., E 58

Aster pilosus Willd., P 35979

Bidens pinnata L., P 35979

Conyza canadensis (L.) Cronq., P 36035

Eupatoriadelphus purpureus (L.) R. M. King, & H. Rob., P 36052

Eupatorium serotinum Michx., P 36039

Helianthus divaricatus L., P 36006

Heterotheca subaxillaris (Lam.) Britt. & Rusby, P 35986

Lactuca canadensis L., P 36050

Lactuca floridana (L.) Gaertn., P 36020

Rudbeckia hirta L., P 35993

APPENDIX
Continued.

Solidago canadensis L., P35991
Solidago gigantea Ait., E 51

BERBERIDACEAE

Podophyllum peltatum L., P 36683

BIGNONIACEAE

**Catalpa bignonioides* Walt., P 37357

BORAGINACEAE

**Buglossoides arvensis* (L.) I. M. Johnston, P 36696
Hackelia virginiana (L.) I. M. Johnston, P 35994

BRASSICACEAE

**Alliaria petiolata* (Bieb.) Cavara & Grande, P 36673
Arabis glabra (L.) Bernh., P 36730
**Capsella bursa-pastoris* (L.) Medik., P 36693

CAESALPINIACEAE

Gleditsia triacanthos L., P 36056

CANNABACEAE

**Cannabis sativa* L., P 36029
Humulus lupulus L., P 36019

CAPRIFOLIACEAE

**Lonicera maackii* (Rupr.) Maxim., P 36682
Sambucus canadensis L., P 36051

CARYOPHYLLACEAE

**Arenaria serpyllifolia* L., P 36691
**Cerastium pumilum* Curtis, P 36697
**Holosteum umbellatum* L., P 36702
**Saponaria officinalis* L., P 35983
Silene stellata (L.) Ait. F., P 36009

CELASTRACEAE

Celastrus scandens L., P 36048

CHENOPODIACEAE

**Chenopodium album* L., E 49

CORNACEAE

Cornus drummondii C. A. Mey., P 36007

CORYLACEAE

Corylus americana Walt., P 36065

EBENACEAE

Diospyros virginiana L., P 37361

ELAEAGNACEAE

**Elaeagnus umbellata* Thunb., P 36723

EUPHORBIACEAE

Acalypha gracilens Gray, P 35974
Acalypha virginica L., P 35975
Chamaesyce nutans (Lag.) Small, P 36053
Croton glandulosus L., P 35973
Phyllanthus caroliniensis Walt., P 36059
Poinsettia dentata Michx., E 52

FABACEAE

**Medicago lupulina* L., P 36726
**Melilotus albus* Medic., P 35992
**Robinia pseudoacacia* L., P 37297

FAGACEAE

Quercus velutina Lam., P 36070

GROSSULARIACEAE

Ribes missouriense Nutt., P 36012

HYDROPHYLLACEAE

Ellisia nyctelea (L.) L., P 36681

JUGLANDACEAE

Carya cordiformis (Wangenh.) K. Koch, P 36026
Carya illinoensis (Wangenh.) K. Koch, P 36063
Carya texana Buckl., P 36001
Carya tomentosa (Poir.) Nutt., P 36018
Juglans nigra L., P 36071

LAMIACEAE

Agastache nepetoides (L.) Ktze., P 36008
**Leonurus cardiaca* L., P 36722
**Nepeta cataria* L., P 36005
Teucrium canadense L., P 36055

LAURACEAE

Sassafras albidum (Nutt.) Nees, P 36000

MALVACEAE

Callirhoë triangulata (Leavenw.) Gray, P 35970

MOLLUGINACEAE

**Mollugo verticillata* L., P 36038

MORACEAE

**Maclura pomifera* (Raf.) Schneider, P 36066
**Morus alba* L., P 36045
Morus rubra L., P 36046

APPENDIX
Continued.

NYCTAGINACEAE

**Mirabilis nyctaginea* (Michx.) MacM., P 35996

ONAGRACEAE

Circaea lutetiana L., P 36024*Oenothera biennis* L., P 36042*Oenothera laciniata* Hill, P 36704

OXALIDACEAE

Oxalis stricta L., P 35989

PHRYMACEAE

Phryma leptostachya L., E 56

PHYTOLACCACEAE

Phytolacca americana L., P 35984

PLANTAGINACEAE

Plantago rugelii Decne., P 35997*Plantago virginica* L., P 36731

POLYGALACEAE

Polygala verticillata L., P 35971

POLYGONACEAE

Antenoron virginianum (L.) Roberty & Vautier, P 36030*Fallopia scandens* (L.) Holub., E 50*Persicaria punctata* (Ell.) Small, P 36028

PORTULACACEAE

Claytonia virginica L., P 36686

RANUNCULACEAE

Anemone virginiana L., P 36037*Ranunculus abortivus* L., P 36687

ROSACEAE

Fragaria virginiana Duchesne, P 36689*Geum canadense* Jacq., P 35995*Prunus serotina* Ehrh., P 36067*Rosa carolina* L., P 36724**Rosa multiflora* Thunb., E 54*Rubus flagellaris* Willd., P 36698*Rubus occidentalis* L., P 36706*Rubus pensylvanicus* Poir., P 36705

RUBIACEAE

Galium aparine L., P 36675

RUTACEAE

Zanthoxylum americanum Mill., P 37359

SCROPHULARIACEAE

Penstemon pallidus Small, P 36703*Scrophularia lanceolata* Pursh, P 36027**Verbascum thapsus* L., P 36033*Veronica arvensis* L., P 36694

ULMACEAE

Celtis occidentalis L., P 36002*Ulmus americana* L., P 37358*Ulmus rubra* Muhl., P 36044

URTICACEAE

Laportea canadensis (L.) Wedd., P 36022

VERBENACEAE

Verbena stricta Vent., P 36015*Verbena urticifolia* L., P 36069

VIOLACEAE

Viola pratincola Greene, P 36684**Viola rafinesquii* Greene, P 36072*Viola sororia* Willd., P 36695

VITACEAE

Vitis aestivalis Michx., P 36034*Vitis riparia* Michx., P 36060

MONOCOTYLEDONEAE

ARACEAE

Arisaema triphyllum (L.) Schott, P 36685

COMMELINACEAE

**Commelina communis* L., P 35988*Tradescantia ohiensis* Raf., P 35987

CYPERACEAE

Carex blanda Dewey, P 36678*Carex festucacea* Schk., P 36707*Carex grisea* Wahl, P 36679*Cyperus lupulinus* (Spreng.) Marcks var. *macilentus* (Fern.) Marcks, P 35982

JUNCACEAE

Juncus tenuis Willd., P 36041

APPENDIX
Continued.

LILIACEAE

Lilium michiganense Farw., P 36061
**Ornithogalum umbellatum* L., P 36676
Smilacina racemosa (L.) Desf., P 36014
Smilacina stellata (L.) Desf., P 36013

POACEAE

**Bromus inermis* Leyss., P 36068
**Bromus tectorum* L., P 36688
**Dactylis glomerata* L., P 36725
**Digitaria sanguinalis* (L.) Scop., P 36040
Elymus villosus Muhl., P 36043
Elymus virginicus L., P 36025
Eragrostis spectabilis (Pursh) Steud., P 35985

Festuca subverticillata (Pers.) E. B. Alexeev., P 36057
Hordeum pusillum Nutt., P 36727
Leersia virginica Willd., P 36061
Muhlenbergia frondosa (Poir.) Fern., E 55
Muhlenbergia schreberi J.F. Gmel., P 36032
Paspalum bushii Nash, P 35976
**Poa pratensis* L., P 36699
Poa sylvestris Gray, P 36677
**Setaria faberi* R.A.W. Herrm., P 35998
Tridens flavus (L.) Hitchc., P 35981

SMILACACEAE

Smilax tannoides L., P 36004
Smilax lasioneuron Hook., P 36054