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Effects of disturbance on the floristic composition and functional ecology of the herbaceous layer in central hardwood forests of Iowa

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Effects of disturbance on the floristic composition and functional ecology of the herbaceous layer in central hardwood forests of Iowa

by

Michaeleen E Gerken

A thesis submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of
MASTER OF SCIENCE

Major: Forestry (Forest Biology)

Program of Study Committee:
Janette R. Thompson, Major Professor
Cathy M. Mabry McMullen
Donald R. Farrar
Ted B. Bailey

Iowa State University
Ames, Iowa
2005

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Graduate College
Iowa State University

This is to certify that the master’s thesis of

Michaeleen E Gerken

has met the requirements of Iowa State University

Signatures have been redacted for privacy
DEDICATION

This is dedicated to those who have offered me inspiration, guidance, and unconditional support. Thank you.

May we never stop learning.
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ABSTRACT

Human impacts have altered the natural landscape throughout much of the Midwestern United States. Iowa, in particular, has undergone extensive land use conversion of prairies, wetlands, and forests to agricultural and to a lesser extent, urban uses. This thesis examined how ecosystem composition and function of herbaceous plants of central hardwood forests in Iowa are impacted as the result of human activities.

We used a variety of floristic quality metrics to compare the species composition of central hardwood forests under different land uses. Although few differences were seen between preserved forests and those that had been managed for single-tree timber harvest, composition of forests adjacent to urban housing subdivisions can shift from habitat specialists (species with affinity for closed-canopy, moist sites; species with a high coefficient of conservatism) to habitat generalists within ten years of development.

We also compared the functional capacity of intact forests with those that have been subjected to disturbance such as grazing, and found greater proportions of native, early-flowering, closed-canopy, and conservative species in intact sites, although there was no difference in total species richness. We found that the nutrient sequestration of the herbaceous layer is greater on intact sites. Disturbed sites have lower biomass and thus nutrient sequestration capacity, in large part because they lack a diverse group of spring ephemerals.

Floristic quality metrics were used to provide a more complete look at composition of the flora, as well to provide a tool for site evaluation, to determine which areas and species are most sensitive and in need of immediate protection and management. Understanding which species and functional groups are key players in nutrient sequestration in central
hardwood forests can help in the creation of systems that better mimic high quality natural systems.
CHAPTER 1: INTRODUCTION

The landscape of the Midwestern United States has undergone dramatic change since human settlement 150 years ago. Prairies, wetlands, and forests have largely been replaced by row crops, pastures, and to a lesser extent, urban developments (Jungst et al., 1998; Bishop et al., 1998). Fertilizer inputs from the agricultural landscape as well as runoff from cleared fields and developed areas, has led to nutrient loss from a formerly almost closed nutrient cycle. Polluted waterways and the resultant hypoxic zone in the Gulf of Mexico are caused by the runoff of excess nutrients, especially nitrogen, in areas that no longer have perennial vegetation to absorb the increased inputs (Mitsch et al., 2001).

The Iowa landscape, in particular, has undergone extensive conversion. For example, forests in Iowa once covered up to 2.7 million ha of the land area (Jungst et al., 1998). After a major initial decline due to harvesting and land conversion, and subsequent reforestation efforts and secondary succession, current estimates indicate that approximately 1.05 million ha of forests remain (Leatherberry et al., 2003). These remaining forests are concentrated in the eastern and southern portions of the state, as well as along waterways as gallery forest (Thompson, 1992).

Iowa forests are categorized as central hardwoods, including oak-hickory communities on uplands, oak-maple-basswood communities on slopes, and silver maple-green ash-walnut communities on bottomlands (Van der Linden and Farrar, 1984). The herbaceous layer of central hardwood forests is diverse, with a characteristic group of spring ephemerals including Allium tricoccum, Podophyllum peltatum, Dicentra cucullaria, Claytonia virginica, and Isopyrum biternatum, as well as early-flowering but summer persistent species Hydrophyllum virginianum, Arisaema triphyllum, and Asarum canadense.
Typical aestival herbaceous plants include *Aster sagittifolius*, *Athyrium filix-femina* var. *angustum*, *Circaea lutetiana* ssp. *canadensis*, *Cryptotaenia canadensis*, *Sanicula gregaria*, *Laportea canadensis*, and *Impatiens capensis* (Eilers and Roosa, 1994).

Remnant natural areas are of great importance to preserve native biodiversity and ecosystem function, but many are currently under intense pressure from human impacts. For example, fragmentation and conversion of natural vegetation to other uses may lead to biodiversity loss, interruption of biogeochemical processes and hydrologic cycles, and climate change (Meyer and Turner, 1992). Human disturbance may negatively impact composition (Moffatt et al., 2004) and thus function of natural areas (Tilman et al., 1997). Increased human activity has been associated with loss of habitat specialists, especially forest interior species (Drayton and Primack, 1996).

The herbaceous layer of forests comprises a large portion of their biodiversity and evidence suggests it is important to maintain ecosystem function. In particular, herbaceous perennials may make up only a small fraction of the biomass of a forest but they can be very important to nutrient uptake. In one of the first studies to recognize this, clear-cutting and herbicide application at the Hubbard Brook ecosystem in New Hampshire resulted in dramatic losses of nutrients from the system (limited capacity of the forests to retain nutrients) (Borman et al., 1968). Furthermore, nutrient uptake by a single guild of herbaceous plants, spring ephemerals, is sufficient to affect cycling at the system level (Blank et al., 1980). Moreover, there is evidence that diversity and species composition of the community affects function. For example, research on grasslands shows that increased diversity of herbaceous plants can increase nutrient uptake and use (Tilman et al., 1997;
Hooper and Vitousek, 1998), but it is unclear whether parallel patterns are found in the herbaceous layer of forests.

Human impacts such as urbanization and agricultural uses can also negatively impact forest composition and function (Tilman et al., 1997; Moffatt et al., 2004). Site preparation and construction of traditional urban housing subdivisions often involves destruction of the native vegetation and seedbed and replanting with non-native ornamentals and turf (McKinney, 2002). Even when remnant flora survives, construction practices have negative effects on the forest community, including increased potential for invasion by exotic species (Pyle, 1995), increased herbivory, and changes in microclimate such as increased insolation, wind, and temperature (Saunders et al., 1991). The agricultural practice of cattle grazing in remnant forests in Iowa can result in soil compaction and reduced moisture availability (Kucera, 1952), as well as shift species composition towards exotics and weedy native species (Mabry, 2002). Early-flowering herbaceous species, including *Arisaema triphyllum*, *Asarum canadense*, *Claytonia virginica*, *Dicentra cucullaria*, *Geranium maculatum*, *Sanguinaria canadensis*, and *Viola pubescens* are among those most vulnerable to disturbance such as grazing (Mabry, 2002). Often as habitat is degraded by human activities, forest species that specialize on the relatively cool, moist habitat of forest interiors are replaced by generalists (Drayton and Primack, 1996).

Natural forested ecosystems are able to slow and filter runoff (Peterjohn and Correll, 1984). Constructed forest systems, including riparian buffer strips, have also been shown to be effective in slowing sediment movement and reducing nutrient inputs to waterways (Lowrance et al., 1984; Mitsch et al., 2001; Schultz et al., 2004). However, these built systems often have limited species biodiversity compared to remnant natural systems, and it
is unclear how a more diverse group of native perennials may affect the efficacy of these buffer strip systems. In Iowa, where what little remains of natural forest systems has often been subjected to disturbance, understanding how to restore degraded natural systems and create built systems that can function more like intact natural systems has the potential for high ecologic value.

*Study Objectives*

The objectives of this research were twofold. First, a variety of floristic quality metrics were used to determine if there were compositional differences in herbaceous species present in forests that had been exposed to different land uses (e.g. grazing, timber management, urbanization, and preserved areas). Second, we harvested plant material to assess whether compositional differences between the herbaceous layer of intact and disturbed forests resulted in differences in nutrient capturing by those systems.

*Thesis Organization*

This thesis is organized into four major parts. The first chapter is a general introduction, the second chapter is a manuscript entitled “Floristic Composition of Central Hardwood Forests in Preserved, Managed, and Developed Areas in Eastern Iowa”, the third chapter is a manuscript entitled “Nutrient Uptake by the Herbaceous Layer in Disturbed and Intact Hardwood Forests in Central Iowa, USA”, and the fourth chapter is a discussion and general conclusion.

*Literature Cited*


Eilers, L.J. and D.M. Roosa. 1994. The vascular plants of Iowa. Univ. of Iowa Press, Iowa City, IA.


CHAPTER 2: FLORISTIC COMPOSITION OF CENTRAL HARDWOOD FORESTS IN PRESERVED, MANAGED, AND DEVELOPED AREAS IN EASTERN IOWA

A paper to be submitted to Forest Ecology and Management

Michaeleen E Gerken, Janette R. Thompson, Cathy M. Mabry

Abstract

Human activities have had dramatic impacts on North American forest ecosystems since Euro-American settlement. We examined relationships between land use of forest areas (forest preserves, managed forests, and urban-proximate forests) and species composition of central hardwood forests. Census surveys of 20 m² forest plots were conducted three times during the growing season for each category of land use in the Cedar Rapids, IA, area. Data were analyzed to determine if species richness, number of native species, coefficient of conservatism, flowering phenology, and habitat specialization differed between land uses. Forests managed for timber harvest (single-tree selection) did not differ from preserved forests. However, in as little as 10 years, development-proximate forests had lower species richness than managed forests, fewer native species, fewer early-flowering species, fewer habitat specialists (species associated with closed-canopy and moist forest), and fewer species with high coefficients of conservatism than either preserved or managed forests. Although upland and midslope positions differed from bottomlands for some attributes, there were no interactions between land use and slope position, providing evidence that the effects of land use are consistent across topographic positions. Results suggest that urban development quickly disrupts floristic composition of forests, causing a shift from specialist to generalist species.
Introduction

Anthropogenic land use change is a global issue. Natural landscapes are subject to numerous changes that include vegetation clearing, water drainage, cultivation and intensification of agricultural production, and urban/suburban/exurban development (Meyer and Turner, 1992). Fragmentation and conversion of natural systems may have overarching implications for loss of native biodiversity, interruption of biogeochemical processes and hydrologic cycles, and climate change (Meyer and Turner, 1992). In the Midwestern United States, agriculture and increasingly mechanized production systems have been leading causes of landscape change (Jackson, 2002). Iowa, in particular, has an intensively managed landscape directed toward agricultural production, which has undergone dramatic reductions in areas of natural vegetation (USDA-Forest Service, 2005). Remnant natural areas in this landscape have value for preserving biodiversity and ecosystem functions such as protection of water quality and nutrient cycling (Saunders et al., 1991).

Land area of Iowa was 15% forested before settlement (Jungst et al., 1998). Iowa forests, which can be characterized generally as central hardwoods, were concentrated primarily in the eastern and southern portions of the state and along rivers and streams (Thompson, 1992). The most recent estimates indicate that about 30% of the original forest area remains (Jungst et al., 1998), and that less than 12% of forested land in Iowa is in public reserves (USDA-Forest Service, 2005). Privately owned forests may be subjected to several forms of land use, including timber harvest and urban development, which can influence species richness (Jenkins and Parker, 1999, 2000), biodiversity (Franklin, 1993), cover (Fredericksen et al., 1999), and floristic composition (Saunders et al., 1991; Moffatt et al., 2004).
Timber management can affect forest composition. Bottomland forests with intensive
disturbance have greater species richness of the herbaceous layer than plots with single-tree
selection and reference stands (Jenkins and Parker, 2000). While harvesting intensity may
not influence richness and diversity, it can promote disturbance-adapted or shade-intolerant
species in northern hardwood forests (Fredericksen et al., 1999). Plots under group or single-
tree selection or reserved areas had a lower proportion of early successional species and of
exotic species than plots with more intensive disturbance in mixed conifer forests (Battles et
al., 2001). Selective harvest had minimal effect on floristic composition of a forest (Jenkins
and Parker, 1999), and Franklin (1993) suggested this system can help promote biodiversity.

Urban land uses have led to increasing encroachment on existing forest remnants,
which may alter forest composition and function (Moffatt et al., 2004; Tilman et al., 1997).
Site preparation and construction of traditional urban housing subdivisions often involve
destruction of native vegetation, removal of the topsoil and seedbed, and subsequent
replanting with nonnative ornamental plants and turf (McKinney, 2002). Decrease in interior
area of remaining forest remnants has a negative effect on the remnant flora, including
increased potential for invasion by exotic species (Pyle, 1995), increased herbivory, and
changes in microclimate. Increased insolation, wind, and temperature lead to losses of
forest-specialist species (Saunders et al., 1991). Urban-proximate forests often are subject to
frequent use and trampling by humans, which also can negatively impact diversity of native
taxa, particularly for forest-specialist species (Moffatt et al., 2004; Drayton and Primack,
1996).

Land-use effects may vary with differences in soils, microclimate, and topography
(Saunders et al., 1991). Drayton and Primack (1996) note that slopes and uplands are often
subject to human visitation and thus disturbance and introduction of exotic plants. Topography influences floristic composition, and fragmentation can magnify the effects of position when hydrology, soil erosion, run-on and run-off, and seed movement are considered (Saunders et al., 1991). Information on how forest land use, i.e., management or development regime, and topographic gradient affect floristic composition will aid in management and development planning.

Measuring floristic change also is complicated because no single measure can capture the complexity involved in diversity (Small and McCarthy, 2002). For instance, while the herbaceous layer is very vulnerable to disturbance (Duffy and Meier, 1992; Robinson et al., 1994) and can thus serve as a possible indicator of site quality and ecosystem function, information on woody vegetation should not be disregarded. Measures of species richness alone are not sufficient for assessing changes because richness does not distinguish between native and exotic species, habitat generalists and specialists, nor species with different functional roles. Floristic metrics based on species conservatism (Swink and Wilhelm, 1994) and analyses of habitat specialization of species (Drayton and Primack, 1996), functional composition (Tilman et al., 1997), and species richness provide a more valid assessment of the flora.

We focused on vascular-plant assemblages in central hardwood forests in eastern Iowa. Our main objectives were to: 1) examine relationships between land use (preserved, managed, or urban housing development-proximate) and species richness, nativeness, phenology, habitat-specialization characteristics of herbaceous plants, and species conservatism in forests in the Cedar Rapids area; and 2) examine relationships between
topographic position (upland, midslope, or bottomland) and the same floristic metrics for these land-use categories.

**Materials and Methods**

**Study area**

The Cedar Rapids metropolitan area is one of the most rapidly growing urban areas in Iowa, increasing 13.6% in population from 1990 to 2000 to approximately 192,000. Linn County, where Cedar Rapids is located, has the third-highest population and housing-unit densities in the state (U.S. Census Bureau, 2005). Because of its location along the Cedar River corridor in the eastern portion of the state, large portions of the Cedar Rapids area consisted of central hardwoods, dominated by *Quercus alba* L., *Quercus rubra* L., *Tilia americana* L., and *Acer saccharum* L. before European settlement and development (Thompson, 1992). Remnant gallery forests are an important part of urban and rural biodiversity in this landscape.

**Study sites**

We conducted census assays of 20 m² plots in preserved, managed, and development-proximate forest sites in the Cedar Rapids, IA, area. Each plot was visited three times over the course of the growing season in April, late June, and late August to allow examination of early spring, mid-season, and late-season flora over three years. Sites were visited only three times each, but these visits were spread over the course of three years due to the time it took to locate sites that met all of the criteria for inclusion.

Site selection criteria were: the remnant had a minimum size to support at least two 20 m² plots in a forest interior setting and had not been farmed or grazed for at least 30 years. Four forested areas were chosen as development-adjacent sites with the additional criterion...
that the remnant was within or adjacent to a subdivision developed within the past 10 years. Urban forest areas were located in subdivisions in the southeastern and northeastern areas of the city. Rural, managed sites were chosen with the additional criterion that the remnant had been logged selectively for partial removal within the past 10 years. Preserved sites were located in Palisades-Kepler State Preserve southeast of the Cedar Rapids metropolitan area, Wickiup Hill Conservation Area of Linn County northwest of the metropolitan area, and Dudgeon Lake State Wildlife Management Area and Hoefler-Dulin Preserve of Benton County, both northwest of the metropolitan area. These preserved sites were chosen with the stipulation that the preserve had not been logged for at least 30 years.

Plot selection and variables measured

At each of the three managed and three preserved sites, we established six plots: two upland, two midslope, and two bottomland plots. Due to a lack of development in bottomland areas, developed sites had only two each of upland and midslope plots (Table 1). We used 20 m² plots to allow for a maximum observation of species present without crossing topographic gradients. Plots were located in forest interiors to minimize edge effects.

We identified all species of vascular plants present in each plot based on Gleason and Cronquist (1991). To assess the relationship of forest management and topographic location to floristic quality metrics, plants were coded according to Drayton and Primack (1996). All plants were identified as either native to Iowa or nonnative. Herbaceous plants were coded as beginning flowering from March to May or June to September. All plants were coded by affinity for closed-canopy sites exclusively, e.g., habitat specialists, versus occurrence in closed or open canopy. All plants were coded by affinity for moist sites exclusively, e.g., habitat specialists, versus occurrence in moist or dry sites. These characters
were assigned to species based on description in two floras of the region (Gleason and Cronquist, 1991; Barkley, 1986). Each native species was assigned a coefficient of conservatism according to a system for rating species quality developed by Swink and Wilhelm (1994) and adapted for the Iowa flora (Iowa State University Ada Hayden Herbarium, 2004). Species were assigned a number from 0 to 10, with the least conservative (lowest values) species able to persist in human-created habitats, and the most conservative species with a high affinity for intact native habitat. We collapsed the ten categories into four for data analysis. Species with a coefficient of conservatism of 0, 1, or 2 were grouped into a new category, 1, generalist species. All native plants with a coefficient of conservatism of 7, 8, 9, or 10 were assigned to a new category, 4, specialist species. Species in the middle categories were not included in this portion of the analysis.

Data analyses

Analyses were performed using two distinct data sets due to the lack of development-adjacent bottomlands (Table 1). Preserved, managed, and development-adjacent forests were compared, combining upland and midslope positions to determine differences related to land use. Likewise, preserved and managed plots were combined to compare upland, midslope, and bottomland positions to determine differences that could be attributed to slope position. Analysis of variance for each data set and Fisher's Least Significant Difference (LSD) tests were conducted using DataDesk® Version 6 software (1997). The independent variables in the model were land use and topographic location. The dependent variables were species richness, nativeness, flowering phenology, affinity for closed canopy, affinity for moist sites, coefficient of conservatism category 1, and coefficient of conservatism category 4. Factors were fixed, and no transformations were made.
Results

We identified 186 plant species in preserved plots, 192 species in managed plots, and 133 species in plots adjacent to recent urban housing developments. We catalogued 173 species in upland plots, 178 species in midslope plots, and 158 species in bottomland plots. Overall, there were 260 species identified across all plots.

Land use

Our analysis of land use is the comparison of preserved, managed, and development-adjacent plots (Table 1). Upland and midslope positions were pooled because there was no interaction between forest type and topographic position (data not presented). Preserved and managed-forest plots did not differ for the floristic metrics (Table 2). Preserved and managed-forest plots did not differ in species richness, but managed plots had greater species richness than development-adjacent forests ($P \leq 0.001$) (Table 2). Development-adjacent plots had fewer native species ($P \leq 0.002$), fewer early-flowering species ($P \leq 0.001$), fewer habitat specialists (closed-canopy ($P \leq 0.005$) or site moisture ($P \leq 0.0001$)), and fewer species with a coefficient of conservatism in category 4 ($P \leq 0.05$) than preserved or managed-forest plots (Table 2). There was no difference in the number of native species with a coefficient of conservatism in category 1 (Table 2).

Proportional data (not shown) followed a similar pattern. Preserved plots had a greater proportion of early-flowering herbs ($P \leq 0.05$) than managed plots.

Topographic location

Our analysis of topographic location is the comparison of upland, midslope, and bottomland plots (Table 1); preserved and managed forests were pooled because there was no
interaction between forest type and topographic position. Upland and midslope positions did not differ for floristic metrics (Table 3). Bottomland plots had lower species richness than other positions ($P \leq 0.0001$, Table 3). Bottomland plots had fewer native species ($P \leq 0.0001$), fewer early-flowering herbs ($P \leq 0.001$), fewer habitat specialists (closed-canopy ($P \leq 0.0001$) or site moisture ($P \leq 0.001$)), and fewer native plants with a coefficient of conservatism in category 4 ($P \leq 0.0001$) than the mean of upland and midslope plots (Table 3). Native species with a coefficient of conservatism in category 1 did not differ among positions (Table 3).

Proportional data (not shown) were similar for most characteristics. Bottomland plots had a greater proportion of species with a coefficient of conservatism in category 1 ($P \leq 0.05$) than upland or midslope plots. Bottomlands also had a greater proportion of species with moist-site affinity and a lower proportion of species with early-flowering phenology ($P \leq 0.05$) than uplands.

Discussion

Preserved, managed, and development-adjacent forests differ in composition. These differences likely are due to human impacts. Use of several floristic quality metrics and analysis along a topographic gradient provide a clearer picture of system dynamics in relation to human impacts. Our use of species richness, nativeness, flowering phenology, habitat affinity, and coefficient of conservatism all point to a loss of specialist species and an increase in generalists with more intense human land use and from upland to bottomland topographic positions.

While there is no single standard in place for how to “qualitatively” assess the flora of a forest, several common tests have been used including species richness, proportion of
natives versus nonnatives, and composition. Combinations of these and other tests reveal floristic patterns for comparison. Richness, Shannon-Weiner diversity, and composition, especially as unique or native, were used to assess pine and hardwood forests in Wisconsin (Brosofske et al., 2001). Species number, composition, and commonness or rareness were used to describe the herbaceous layer of southern Appalachian hardwood forests (Meier et al., 1995). Nativeness, commonness, habitat-affinity categories, and life-history characteristics (woody versus herbaceous, annual versus perennial, and mode of fruit dispersal) were used to describe the Staten Island, NY flora (Robinson et al., 1994). For this study preserved areas served as a reference for compositionally diverse, relatively intact forests, with minimal human impacts (Norris and Farrar, 2001).

**Land use**

State and county preserves served as references for intact, mature central hardwood stands in this area. Our results indicate that single-tree selection management showed no deleterious effects on the flora in these systems, in comparison with preserved forests. This corroborates evidence presented by Battles et al. (2001) on species richness, seral stage, and proportion of nonnatives in mixed conifer systems and by Jenkins and Parker (1999) on composition, Shannon-Weiner diversity, and richness in central hardwood systems. Selective harvest can maintain structural diversity of a forest (Brosofske et al., 2001) and provide canopy gaps for seedling establishment (Meier et al., 1995) without negative impacts on other flora. In comparison of adjoining forests subjected to selective harvest and intensive logging, the intensive disturbance changes composition of the herbaceous layer by removing less common and rare species (Meier et al., 1995).
Forests adjacent to urban housing developments underwent changes in herbaceous species composition, richness, and quality within ten years after disturbance. Specialist species were disproportionately lost and generalists became more prevalent. A lower proportion of native species were observed in development-proximate areas, indicating an increase in exotic species (Table 2). Areas with extensive anthropogenic soil disturbance experience changes in composition including lowered richness of native and rare species and increases in number of nonnatives (McIntyre and Lavorel, 1994). Compositional shifts are likely related to increased potential for invasion by nonnative species, herbivory, and changes in microclimate associated with fragmentation (Saunders et al., 1991). As forests become more fragmented, interior habitat for specialist species becomes scarcer and small populations may face local extinctions (Robinson et al., 1994).

**Topographic location**

While Robinson et al. (1994) observed that losses of native species in an urbanizing area were not habitat-specific for wet versus dry areas, our results suggest that habitat position is an important factor in central hardwood forests. Upland and midslope positions have greater species richness and higher proportions of specialist species, whereas bottomland communities are less rich and have more exotics and generalist species (Table 3). Richness of rare species declines from upper slope to lower slope positions (McIntyre and Lavorel, 1994). The significance of habitat position is especially important in light of findings of vulnerability of slope and ridge communities to human impacts (Drayton and Primack, 1996). Bottomlands are generally not zoned for urban development but are still susceptible to disproportionate loss of native species inhabiting moist sites (Drayton and Primack, 1996), possibly due to vulnerability to microclimatic and hydrological changes.
With the rapidly spreading influence of urbanization, it is important to determine how remnant forests are affected, which areas and species are most sensitive and most in need of immediate protection and management. This study provides baseline data for future efforts to monitor changes in floristic composition in a rapidly urbanizing area. Long-term monitoring could answer the questions of whether compositional shifts in urban areas are permanent, if they are progressive, and what steps can be taken during development and through forest management practices to mediate species losses.

In a landscape dominated by human use, Iowa’s forests are subject to a variety of disturbances, from minimal (public preserves and selectively harvested private lands) to severe (urbanization and affected adjacent remnants). Inherent complexities such as topography make forest ecosystems dynamic and can compound human impacts. Floristic metrics that include a variety of indices can help in evaluation of the intertwined effects of land use and topography on floristic composition. Management techniques may in fact protect native biodiversity and sensitive areas such as species-rich uplands and midslopes. This study showed that intense human use has negative effects on specialist species, possibly leading to biotic homogenization at a landscape level.

Acknowledgements

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assistance with this project. We also thank Troy Bowman and Matt Latiolais for their assistance in the field.

**Literature Cited**


Table 1. Number of plots surveyed in the Cedar Rapids, Iowa, area in preserved and managed forests across upland, midslope, and bottomland topographic positions and for forests adjacent to recent urban housing developments across upland and midslope positions. Three sites were identified for each land-use type and two plots identified at each topographic position of each site; development-adjacent midslopes included one site with only one plot and two sites with three plots each. No plots or sites were identified for bottomland forests adjacent to development.

<table>
<thead>
<tr>
<th>Topographic location</th>
<th>Preserved</th>
<th>Managed</th>
<th>Development adjacent</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upland</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>18</td>
</tr>
<tr>
<td>Midslope</td>
<td>6</td>
<td>6</td>
<td>7</td>
<td>19</td>
</tr>
<tr>
<td>Bottomland</td>
<td>6</td>
<td>6</td>
<td>-</td>
<td>12</td>
</tr>
<tr>
<td>Total</td>
<td>18</td>
<td>18</td>
<td>13</td>
<td>49</td>
</tr>
</tbody>
</table>
Table 2. Mean number of species per plot for floristic metrics for preserved and managed forests and forests adjacent to recently built urban housing developments in the Cedar Rapids, IA, area. Values are means for upland and slope plots for 13 plots in development-adjacent forests, and 12 plots each in preserved and managed forests. Means with the same character within each metric are not different at $P \leq 0.05$ according to Fisher’s LSD test. Numbers in parentheses are one standard deviation of the mean.

<table>
<thead>
<tr>
<th>Land use</th>
<th>Species richness</th>
<th>Native</th>
<th>Early-flowering</th>
<th>Site affinity</th>
<th>Coefficient of conservatism</th>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>Closed-canopy</td>
<td>Moist</td>
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<td>53.6a (6.6)</td>
<td>22.7a (4.7)</td>
<td>27.6a (5.3)</td>
<td>31.8a (5.7)</td>
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<tr>
<td>Managed</td>
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<td>57.6a (6.6)</td>
<td>21.3a (2.8)</td>
<td>28.5a (4.3)</td>
<td>33.8a (4.0)</td>
</tr>
<tr>
<td>Development-adjacent</td>
<td>48.0b (8.4)</td>
<td>46.5b (8.3)</td>
<td>15.4b (5.3)</td>
<td>21.9b (5.7)</td>
<td>23.8b (4.9)</td>
</tr>
</tbody>
</table>
Table 3. Mean number of species per plot for floristic metrics for upland, slope, and bottomland positions in preserved and managed forests in the Cedar Rapids, IA, area. Values are means for 12 plots each on uplands, slopes, and bottomlands. Means with the same character within each metric are not different at $P \leq 0.05$ according to Fisher's LSD test. Numbers in parentheses are one standard deviation of the mean.

<table>
<thead>
<tr>
<th>Topographic location</th>
<th>Floristic metrics</th>
<th>Site affinity</th>
<th>Coefficient of conservatism</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Species richness</td>
<td>Native</td>
<td>Early-flowering</td>
</tr>
<tr>
<td>Upland</td>
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<tr>
<td>Slope</td>
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<td>57.2a (6.1)</td>
<td>22.9a (1.9)</td>
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<tr>
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<td>37.5b (13.1)</td>
<td>35.8b (13.2)</td>
<td>13.9b (6.9)</td>
</tr>
</tbody>
</table>
CHAPTER 3: NUTRIENT SEQUESTRATION BY THE HERBACEOUS LAYER IN DISTURBED AND INTACT HARDWOOD FORESTS IN CENTRAL IOWA, USA

A paper to be submitted to the Canadian Journal of Botany

Michaeleen E Gerken, Cathy M. Mabry, Janette R. Thompson

Abstract

North American forests have been subjected to human disturbances that alter the composition and function of these ecosystems. This study was conducted to determine whether relatively intact forests with high biodiversity of native herbaceous perennials have greater nutrient sequestration than forests that have been subjected to disturbance. Census surveys of herbaceous perennials were conducted on 20 m by 20 m plots placed in three central Iowa forests with proximate intact and disturbed forests. Plots were compared according to a set of floristic quality metrics including species richness, proportion of native species, coefficient of conservatism, flowering phenology, and habitat specialization. Above and belowground biomass of herbaceous perennials was harvested from quadrats within the plots in spring and summer, weighed, and analyzed for nitrogen, phosphorous, and potassium content. Disturbed plots generally lacked the presence of a diverse spring ephemeral community with persistent belowground rooting structures that characterized intact plots. Intact plots had greater biomass and thus greater total estimated nutrient sequestration than disturbed plots above and belowground at the time of spring harvest, and belowground in the summer. Herbaceous layer biodiversity, including high quality habitat specialists, can enable an ecosystem to capture more nutrients and store them on site.
Introduction

Throughout North America native plant communities have been replaced by human-dominated systems, resulting in widespread nonpoint nutrient pollution of aquatic systems (Carpenter et al., 1998). For example, removal of prairies, wetlands, and forests from the grain belt region of the Midwestern United States and Central Canada, followed by increased fertilizer inputs in the agricultural landscape that replaced them, has led to waterways polluted by nutrients, especially nitrogen. Ultimately, this has caused rapid expansion of the hypoxic zone in the Gulf of Mexico, in part because insufficient perennial vegetation remains to absorb the increased nutrient inputs (Mitsch et al., 2001). The greatest potential losses of nutrients to streams in temperate areas occur in the spring when high rainfall and snowmelt drive water through systems where plants are either absent (bare cropfields) or dormant (perennial vegetation) (Peterson and Rolfe, 1982).

Increasingly, research points to the capacity of land with perennial vegetation, such as riparian buffers, to slow and filter runoff (Lowrance et al., 1984; Schultz, et al. 2004). The role of hardwood forests in nutrient uptake and retention was first demonstrated by harvest experiments in the Hubbard Brook watershed (Borman et al., 1968). After clear-cutting and application of herbicide, metabolically active plant tissue was greatly reduced and more water passed through the system unfiltered, leading to accelerated nutrient loss (Borman et al., 1968). More recent research on riparian forested areas in agricultural landscapes indicates they retain most incoming nutrients (Jordan et al., 1993; Phillips et al., 1993). For example, a hardwood riparian forest in Maryland retained close to 90% of nitrogen and 80% of phosphorous inputs annually (Peterjohn and Correll, 1984).
While it has been demonstrated in very specific circumstances that increased functional group diversity may increase nutrient resource use (e.g. on a serpentine grassland, Hooper and Vitousek, 1998), similar data is not available for forest herbaceous perennial species. Combined evidence from studies of several different individual species suggest that an intact, diverse understory would likely have the greatest nutrient retention, in part due to the difference in phenology, physiology, and uptake capacities among species (Blank et al., 1980; Peterson and Rolfe, 1982), as well as the proportional biomass of each (Muller, 2003; Tessier and Raynal, 2003). Although herbaceous perennials make up only a fraction of the total biomass of a forest, perennials that are photosynthetically active before tree leaf-out and canopy closure have been shown to absorb nutrients in quantities nearly equal to potential annual losses (Blank et al., 1980; Peterson and Rolfe, 1982; Tessier and Raynal, 2003). However, studies on spring nutrient dynamics have focused on the uptake capacity of a single or small number of vernal species, for example, *Erythronium americanum* (Muller and Borman, 1976), *Allium tricoccum* (Rothstein, 2000), or *Claytonia virginica* (Eickmeier and Schussler, 1993). While this work points to the important role of herbaceous perennials in nutrient retention over a particular time period, their full functional capacity needs to be evaluated based on the entire suite of herbaceous plants present on a site, both vernal and aestival.

Iowa, as part of the intensively agricultural upper Midwest, is particularly well suited for studying the role of forests in the nutrient dynamics of agricultural landscapes. Extensive conversion of land to agricultural uses, including grazing and row-cropping, has reduced forested area in the state by two-thirds (Jungst et al., 1998). Forested remnants tend to be concentrated in the uplands of eastern and southern Iowa, and riparian gallery forests
throughout the state (Thompson, 1992). A majority of the remaining forested land has been disturbed by human activities, particularly cattle grazing, which may eliminate or reduce the abundance of many forest perennial herbaceous species, including a suite of spring-flowering species (Mabry, 2002). The agricultural practice of grazing in remnant forests has been shown to change other site characteristics, including soil and microclimatic features (Kucera, 1952).

Our premise is that native specialist species and a suite of early-flowering perennials are important qualitative characteristics indicative of natural conditions of central hardwoods prior to Euro-American settlement. Preserved areas and areas with minimal human impacts can serve as a reference for high-quality, compositionally diverse, relatively intact forests (Norris and Farrar, 2001).

Intact and degraded remnant forests surrounded by agricultural land found in Iowa provided an ideal setting for our initial investigation into the functional role of herbaceous forest communities in nutrient dynamics within an agricultural landscape. In this study, floristic composition was compared on a limited number of disturbed and intact sites using several metrics because the literature suggested that phenology is an important component of nutrient cycling (Muller and Borman, 1976) and because human disturbance may negatively impact species that specialize on closed-canopy, moist sites (Drayton and Primack, 1996; Saunders et al., 1991). We also compared the nutrient content of the same disturbed and intact herbaceous perennial communities. We specifically hypothesized that the intact forests would differ in floristic composition and would have greater nutrient storage capacity than the more disturbed forests.
Materials and Methods

Study areas

This study was conducted in central Iowa, USA, (41°41'-41°97'N, 92°50'-93°32'W). Remnant central hardwoods are predominantly in riparian gallery forests, characterized by oak-maple-basswood communities (Van der Linden and Farrar, 1984). We identified three central Iowa woodlands where disturbed and intact gallery forests occur in close proximity.

The first area, (Conard Environmental Research Area) was located near Grinnell in Jasper County, IA. It has an intact 19.4 ha forest, dominated by Quercus alba, with Carya ovata, C. cordiformis, Ulmus americana, U. rubra, Celtis occidentalis, Tilia americana, and Ostrya virginiana also present. An adjacent 4.19 ha of forest area was heavily grazed until the 1950s. The canopy closed after grazing ceased and is dominated by Quercus velutina, Juglans nigra, Celtis occidentalis, Ulmus americana, and Prunus serotina (L. Mottl, personal communication). Soils are well- to moderately-well drained and formed in clay loam glacial till (USDA-Soil Conservation Service, 1979).

The second woodland (Robison Wildlife Acres) is a 31.6 ha preserve donated to Story County in 1970. The intact forest area is dominated by Quercus alba, Q. rubra, Tilia americana, Carya ovata, Acer nigrum, and Ostrya virginiana. A portion of the preserve was heavily grazed prior to acquisition (S. Lewka, personal communication). This forest is dominated by Quercus alba, Tilia americana, Fraxinus americana, Ulmus americana, Gleditsia tricanthos, Celtis occidentalis, Prunus serotina, Acer nigrum, and Ostrya virginiana. Soils are well-drained and formed in loamy glacial till (USDA-Soil Conservation Service, 1984).
The third woodland (a privately owned parcel near Ames in Story County) has had active restoration of a forested slope that had been grazed prior to 1965. Woodland herbaceous plants and soil were transplanted from a nearby mature woodland in 1975 into a 0.2 ha area leading to development of rich understory similar to a relatively undisturbed site. The canopy is dominated by *Celtis occidentalis*, *Juglans nigra*, *Prunus serotina*, *Ulmus americana*, and *Acer negundo*. An adjacent forested slope had no restoration, and is dominated by *Acer saccharinum*, *Acer negundo*, and *Fraxinus pennsylvanica* (D. Farrar, personal communication). Soils are well- to poorly- drained and formed in loamy glacial till and local alluvium (USDA-Soil Conservation Service, 1984).

**Plot selection and variables measured**

We had observed these sites and had anecdotally observed qualitative differences. We used a set of floristic quality metrics to quantify these differences. Two paired 20 m² plots, disturbed and intact, were located at each site for a total of six plots. In order to quantify floristic differences among the sites we identified all herbaceous species present in the plot (nomenclature followed Gleason and Cronquist, 1991).

Floristic quality of disturbed and intact sites was compared using seven metrics calculated at the plot level. Species were coded as beginning growth and flowering from April to May (spring species) or June to September (aestival species). Species were coded by affinity for closed-canopy sites exclusively, e.g., habitat specialists, versus occurrence in closed or open canopy, e.g., habitat generalists. Species were also coded by affinity for moist sites exclusively, e.g., habitat specialists, versus occurrence in moist or dry sites, e.g., habitat generalists. These characters were assigned to species based on habitat descriptions from two floras covering the region, Gleason and Cronquist (1991) and Barkley (1986).
Coefficient of conservatism, a system for rating species quality based on their affinity for habitats unaltered by humans (Swink and Wilhelm, 1994) as adapted for the Iowa flora (Iowa State University Ada Hayden Herbarium, 2004), provided an additional metric for evaluating the natural quality of the sites. Species were assigned a number from 0 to 10, with the least conservative species, 0 (able to persist in human-created habitats), and the most conservative species, 10 (with a high affinity for intact native habitat). Because similar categories could not be reliably distinguished ecologically, (for example category 1 from category 2), the ten categories were collapsed into four categories for data analysis. Species were assigned a number from 0 to 10, with the least conservative species, 0 (able to persist in human-created habitats), and the most conservative species, 10 (with a high affinity for intact native habitat). Because similar categories could not be reliably distinguished ecologically, (for example category 1 from category 2), the ten categories were collapsed into four categories for data analysis. Species in the middle categories were not included in the analysis. We also calculated richness of exotic and native species, as well as overall species richness.

Eight 0.25 m² quadrats were placed at three meter intervals on a diagonal transect of each plot. Within each of the eight quadrats we identified species present and harvested all above and below-ground herbaceous plant material, in both a spring harvest (conducted between April 15-25, 2004), and a summer harvest (conducted between June 22-July 6, 2004). In spring, quadrats were randomly assigned to either the right or left side of the transect line. Summer quadrats were harvested from the opposite side. Harvested plants were stored in a cooler, rinsed thoroughly with water, separated into roots and stems, and oven-dried at 65°C for 48 hours. Dried samples were weighed in order to estimate above and below ground biomass. After weighing, a subsample was ground to pass a 20-mesh sieve.
Nutrient analyses of plant tissue samples were performed by the Iowa State University Soil and Plant Analysis Laboratory, Ames, Iowa. Microwave digestion and analyses for nitrogen, phosphorous, and potassium (N, P, and K, respectively) followed Anderson and Henderson (1986). At the time of both harvests, some quadrats had insufficient herbaceous material present to perform digestion. These samples represent missing values and the summer harvest is therefore a comparison of data from 12-16 quadrats from 2 sites and the spring harvest is the comparison of 20-24 quadrats from 3 sites.

To examine whether differences in plant biodiversity, tissue nutrient concentration, or biomass could be attributed to soil nutrient levels, soil samples were collected from the first and last quadrat along the transect in each plot. Soil was cold-stored and then allowed to air-dry for one week. Dried samples were ground to pass a 20-mesh sieve. Nutrient analyses of soil samples were performed by the Iowa State University Soil and Plant Analysis Laboratory, Ames, Iowa. Soil N was extracted by the Dumas method of dry combustion (Bremner, 1996). Soil P and K were extracted using the Mehlich-3 method (Mehlich, 1978).

**Data analyses**

Mean biomass of the eight 0.25 m² quadrats were analyzed. Estimated nutrient sequestration was determined by multiplying the mean plant tissue nutrient concentration of the plot by the mean biomass (converted to kg/ha) of the plot.

Floristic quality metrics were analyzed using one-way analyses of variance where the independent variable in the model was disturbance (treatment) and the dependent variables were the seven floristic quality metrics. Plant biomass, tissue nutrient concentration, estimated nutrient sequestration (kg/ha), and soil nutrients were analyzed with two-way analyses of variance where the independent variables were site (a blocking factor) and
disturbance (treatment), and the dependent variables were biomass, percent tissue concentrations of total N, total P, and total K, and nutrient sequestration. Factors were fixed, and no transformations were needed to normalize the data. All analyses were conducted using DataDesk® Version 6 software (1997). Given the limited replication in this pilot study, we chose a more liberal value of $p = 0.10$ for declaring significance.

**Results**

We compared means for the three sets of disturbed and intact forest plots for floristic quality metrics, biomass, nutrient concentration and estimated nutrient sequestration of herbaceous plants, and soil nutrient levels.

By several different measures, intact plots were floristically of greater quality than disturbed sites. Intact plots had higher proportions of native species ($p \leq 0.01$), early-flowering species ($p \leq 0.01$), closed-canopy specialists ($p \leq 0.05$), and species with coefficients of conservatism in category 4 compared to disturbed plots ($p \leq 0.08$, Table 1).

In the spring, aboveground biomass was more than two times greater and belowground biomass more than four times greater in intact plots than in disturbed plots (Tables 2 and 3). At the summer harvest, belowground biomass of intact plots was still more than three times greater than that of disturbed plots, but aboveground biomass was similar (Tables 2 and 3). Because of large differences between sites within a type and low replication, most differences were statistically significant.

There were few differences in plant tissue nutrient concentration between the disturbed and intact sites (Tables 4 and 5), although aboveground total P concentration was higher in intact plots for both harvests (Tables 4 and 5), and belowground total P concentration was higher in disturbed plots in the spring (Tables 4 and 5).
Estimated total nutrient sequestration by herbaceous species (N, P, and K) was approximately three times greater for intact versus disturbed sites in the spring (Tables 6 and 7). The intact sites also had greater estimated nutrient sequestration belowground in summer (Tables 6 and 7). Again, these differences were not statistically significant due to the limited replication.

Soil nutrient concentration (ppm) did not differ between intact and disturbed sites for N, P, or K (data not presented, ANOVAs yielded $p \geq 0.369$).

**Discussion**

Although we did not examine species level diversity, our results point to the importance of what is often referred to as functional group diversity, e.g. groups of taxonomically distinct species that play a similar role in ecosystem processes (Petchey and Gaston, 2002). The functional role of species composition in terms of biomass and total nutrient sequestration is dependent upon functional group diversity. A variety of floristic quality metrics were used to compare and quantify compositional differences between sites. Although the intact sites had greater overall floristic quality by several metrics, the results primarily point to the importance of early spring flowering species in accounting for the greater nutrient sequestration. Spring ephemerals are easily distinguished as a functionally important group (Muller and Borman, 1976) that can be missing from disturbed sites.

The large difference we observed for herbaceous biomass was largely due to the abundance of early flowering species (above and belowground biomass of spring samples are a direct measure of this) and persistence of their underground storage organs (belowground biomass of summer samples) for intact plots. Because soil and plant tissue nutrient concentration between site types were similar, we conclude that the biomass of spring
ephemerals largely drove the differences in estimated nutrient sequestration that we observed. Spring ephemeral species present on intact plots that were largely absent from disturbed plots included *Allium tricoccum, Dentaria lacinata, Dicentra cucullaria, Claytonia virginica, Erythronium albidum, Isopyrum biternatum,* and *Anenomella thalictroides,* as well as early-flowering but summer persistent species *Hydrophyllum virginianum* and *Hepatica nobilis* var. *acuta.*

The estimated total nutrient sequestration of the intact sites we studied was generally greater than previously reported for studies based on a single species or a subset of the total species. Our study also points to the importance of including the full complement of species present in assessing nutrient dynamics in general and nutrient sequestration in particular. Many studies on spring nutrient dynamics have focused on a single herbaceous species. For example, Hubbard Brook studies showed that *Erythronium americanum* serves as a short-term sink for nutrients. It was estimated that this species can take up 1.0 kg/ha of N and 0.6 kg/ha of K in spring, when losses to streams can be between 1.0-3.0 kg/ha for N and 0.5-1.5 kg/ha for K (Muller and Borman, 1976; Muller, 1978). In Tennessee hardwood systems, early spring uptake by *Claytonia virginica* can equal 17.9 kg/ha of N and 3.1 kg/ha of P aboveground, and 13.1 kg/ha of N and 1.3 kg/ha P belowground (converted from g/m² as reported by Anderson and Eickmeier, 2000). However, as Tessier and Raynal (2003) note, in terms of function of the understory, the community is important as a whole because of differences in phenology and uptake capacities among species (see also Blank et al., 1980; Peterson and Rolfe, 1982).

A limited number of studies have reported on the composition and nutrient dynamics of more complex plant communities. For example, in a study of nutrient uptake of a spring
ephemeral community in south-central Indiana hardwoods, Blank et al. (1980) observed that a suite of six species had N uptake of 5.5 kg/ha, P uptake of 0.10 kg/ha, and K uptake of 4.5 kg/ha (five times the N and seven times the K of *Erythronium americanum* alone). Our estimates of total nutrient sequestration of the entire herbaceous community of intact plots at spring harvest were 35.6 kg/ha of N, 2.9 kg/ha of P, and 40.8 kg/ha of K, a difference of magnitude at least six times greater for each nutrient, and lead us to the conclusion that herbaceous plants may be more important in nutrient cycling, despite their relatively small portion of the total biomass of a forest, than has been previously estimated.

Early spring biomass production and nutrient uptake may capture and retain available nutrients at a time when they are vulnerable to loss from the system because other plants remain dormant. The functional importance of the spring ephemerals in particular has been emphasized by a number of previous investigators (Muller and Borman, 1976; Eickmeier and Schussler, 1993; Rothstein, 2000). Several studies have examined the "vernal dam" hypothesis, which proposes that nutrients are taken up by spring ephemerals and returned via senescence for use by aestival species (Muller and Borman, 1976; Eickmeier and Schussler, 1993; Rothstein, 2000). This study does not prove or disprove that nutrients are cycled in this manner, but our results do indicate that a significant amount of biomass is produced and nutrients taken up in spring and remain stored in belowground root structures of spring-flowering perennials. Muller (1978) notes that for *Erythronium americanum*, net spring biomass production ranged from 113-163 kg/ha, but by summer had dropped only slightly to 77-138 kg/ha, implying that perennial rooting structures can hold a substantial amount of nutrients on-site, even when the aboveground portions of ephemerals are dormant.
This study is unique in that we examined the entire herbaceous layer community, documenting both biomass and nutrient sequestration for intact forest areas paired with adjacent sites subjected to human disturbance. Our study supports earlier assertions that spring-flowering species are important in nutrient uptake and storage before peak activity by woody plants and summer herbaceous species. We observed no difference in the function of aestival species between disturbed and intact plots, but persistent root structures from the spring perennials still present and harvested in summer suggest that intact sites can store greater quantities of captured nutrients and for longer periods of time. The ability of herbaceous perennials, particularly spring ephemerals, to capture and store nutrients points to the potential benefits of restoring these species to disturbed ecosystems and introducing them in systems constructed for such a purpose, such as riparian buffers.

Acknowledgements

This work was supported in part by McIntire-Stennis funds, State of Iowa funds, the Leopold Center for Sustainable Agriculture, and Pioneer Foundation. The authors thank persons who granted permission for plots and harvesting (Larissa Mottl, Steve Lewka, and Don Farrar), and persons who assisted in sample collection and processing (Nettie Spitz, Troy Bowman, and Adam Puderbaugh).

Literature Cited


Table 1. Mean proportion of species per plot for floristic quality metrics for disturbed and intact forests in central Iowa. [Species richness values are mean counts.] Values are means for 3 plots in disturbed forests, and 3 plots in intact forests. Means with the same character within each metric are not different at $P \leq 0.10$ according to Fisher's LSD test. Numbers in parentheses are one standard deviation of the mean.

<table>
<thead>
<tr>
<th>Disturbance</th>
<th>Species richness</th>
<th>Native (%)</th>
<th>Early-flowering (%)</th>
<th>Closed-canopy (%)</th>
<th>Moist (%)</th>
<th>Category 1 (%)</th>
<th>Category 4 (%)</th>
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<tbody>
<tr>
<td>Disturbed</td>
<td>36.3a (2.1)</td>
<td>94.4a (2.7)</td>
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<td>39.3a (9.9)</td>
<td>54.5a (5.3)</td>
<td>16.8a (5.4)</td>
<td>14.4a (10.1)</td>
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<tr>
<td>Intact</td>
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<td>99.0b (1.7)</td>
<td>65.9b (9.2)</td>
<td>49.7b (8.5)</td>
<td>59.5a (3.1)</td>
<td>19.6a (4.4)</td>
<td>19.5b (9.9)</td>
</tr>
</tbody>
</table>
Table 2. Mean biomass (g/0.25m²) of herbaceous plant tissue. Values are means for 8 quadrats within 3 plots in disturbed forests, and 3 plots in intact forests.

<table>
<thead>
<tr>
<th>Biomass (g/0.25m²)</th>
<th>Herbsaceous plant tissue</th>
<th>Spring</th>
<th>Summer</th>
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<tbody>
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<td></td>
<td></td>
<td>Aboveground</td>
<td>Below</td>
</tr>
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<td>Disturbed</td>
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<td>6.03</td>
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<td>Intact</td>
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<td>14.99</td>
<td>24.53</td>
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Table 3. Analyses of variance of herbaceous plant tissue biomass (g/0.25m²) by type and site. Type refers to disturbed or intact forest areas.

<table>
<thead>
<tr>
<th>Biomass</th>
<th>Spring</th>
<th></th>
<th></th>
<th>Summer</th>
<th></th>
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<tr>
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<td>MS</td>
<td>P</td>
<td>Below</td>
<td>df</td>
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<td>8.16</td>
<td>2</td>
<td>156.07</td>
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Table 4. Total N, P, and K concentration (%) of herbaceous plant tissue. Values are means for 3 plots in disturbed forests, and 2 plots in intact forests.

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Spring</th>
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</tr>
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<tr>
<td></td>
<td>Aboveground</td>
<td>Below</td>
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<tr>
<td>Total N (%)</td>
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<td></td>
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<td>Total P (%)</td>
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<td></td>
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<td>Total K (%)</td>
<td>3.78</td>
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<td></td>
<td>3.71</td>
<td>1.91</td>
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Table 5. Analyses of variance for plant tissue nutrient concentration (%) by type and site. Type refers to disturbed or intact forest areas.

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<th>df</th>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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Table 6. Estimated total N, P, and K sequestration (kg/ha) of the herbaceous layer. Values are means for 3 plots in disturbed forests and 3 plots in intact forests for spring, and 2 plots in disturbed and 2 plots in intact forests in summer.

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Spring</th>
<th></th>
<th>Summer</th>
<th></th>
</tr>
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<tr>
<td></td>
<td>Aboveground</td>
<td>Below</td>
<td>Total</td>
<td>Aboveground</td>
</tr>
<tr>
<td>Total N</td>
<td>Disturbed</td>
<td>8.0</td>
<td>4.4</td>
<td>12.4</td>
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<tr>
<td></td>
<td>Intact</td>
<td>20.1</td>
<td>15.5</td>
<td>35.6</td>
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<tr>
<td>Total P</td>
<td>Disturbed</td>
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<td>0.5</td>
<td>0.9</td>
</tr>
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<td>Intact</td>
<td>1.5</td>
<td>1.4</td>
<td>2.9</td>
</tr>
<tr>
<td>Total K</td>
<td>Disturbed</td>
<td>8.5</td>
<td>5.2</td>
<td>13.7</td>
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<tr>
<td></td>
<td>Intact</td>
<td>21.7</td>
<td>19.1</td>
<td>40.8</td>
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Table 7. Analyses of variance of estimated nutrient sequestration of the herbaceous layer (kg/ha) by type and site. Type refers to disturbed or intact forest areas.

<table>
<thead>
<tr>
<th>kg/ha</th>
<th>Spring Aboveground</th>
<th>Spring Below</th>
<th>Summer Aboveground</th>
<th>Summer Below</th>
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<tbody>
<tr>
<td></td>
<td>df</td>
<td>MS</td>
<td>P</td>
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<td></td>
<td></td>
<td></td>
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</tr>
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<td>Total P</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Type</td>
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<td>1.8 x 10^4</td>
<td>0.0613</td>
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<td>0.1797</td>
<td>2</td>
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<td>1.2 x 10^3</td>
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<td>2</td>
</tr>
<tr>
<td>Total K</td>
<td></td>
<td></td>
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<td></td>
</tr>
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CHAPTER 4: CONCLUSIONS

Human impacts have altered the natural landscape throughout much of the Midwestern United States. Iowa, in particular, has undergone extensive land use conversion of prairies, wetlands, and forests. Fragmentation and conversion of natural systems have overarching implications for loss of native biodiversity, interruption of biogeochemical processes and hydrologic cycles, and climate change (Meyer and Turner, 1992). This thesis examined how ecosystem composition and function of herbaceous plants of central hardwood forests in Iowa are impacted as the result of human activities such as agriculture and urbanization.

In comparison of managed and urban-proximate forests with preserved forests, our results indicate that low-impact land use such as single-tree selection timber harvest does not negatively affect species composition and floristic quality metrics. In contrast, composition of forests adjacent to urban housing subdivisions can shift from habitat specialists (species with affinity for closed-canopy, moist sites; species with a high coefficient of conservatism) to habitat generalists within ten years of development. We did not examine the mechanisms of compositional shifts but other studies indicate they may be the result of increased potential for invasion by exotic species, herbivory, and changes in microclimate such as increased insolation, wind, and temperature (Saunders et al. 1991).

Our results suggest that habitat position is an important factor; upland and midslope positions have greater species richness and higher proportions of specialist species while bottomland communities are relatively depauperate and have more exotics and generalist species. The significance of habitat position is especially important in light of findings of
disproportionate loss of native species from moist sites and vulnerability of slope and ridge communities to human impacts (Drayton and Primack 1996).

In comparison of intact forests and those that have been subjected to disturbance such as grazing, we found greater proportions of native, early-flowering, closed-canopy, and conservative species in intact sites, although there was no difference in total species richness. Most importantly, we found that nutrient sequestration of the herbaceous layer is considerably greater on intact sites. Disturbed sites have lower biomass and thus lower nutrient sequestration, in large part because they lack a diverse group of spring ephemerals. Early spring biomass production and nutrient sequestration may be critical in capturing and retaining available nutrients at a time when they are susceptible to loss from the system because other plants remain dormant.

The implications of this research can be practical for both further research and more effective land management. A variety of floristic quality metrics such as species richness, nativeness, flowering phenology, habitat affinity for closed-canopy or moist sites, and coefficient of conservatism can provide information on composition of the flora, as well as provide a tool for site evaluation to determine which areas and species are most sensitive and which are most in need of immediate protection and management. Information on the functional role of herbaceous plants in central hardwood forests can aid in restoration of degraded forests as well as creation of built systems such as riparian buffer strips. Identifying species and functional groups that are key players in nutrient sequestration could be useful to create systems that better mimic high quality natural ecosystems.

In order to integrate natural, agricultural, and urban land uses, we will need to continue to document the role that natural areas play in helping to provide ecosystem
services. In landscapes that have undergone extensive land use conversion such as agriculture and urbanization, preservation and restoration of diverse, functional areas of native vegetation such as forests can provide innumerable benefits.

**Literature Cited**


APPENDIX A: SPECIES LISTS FOR FLORISTIC COMPOSITION OF CENTRAL HARDWOOD FORESTS IN PRESERVED, MANAGED, AND DEVELOPED AREAS IN EASTERN IOWA

Preserved area 1: Palisades-Kepler State Preserve
(uplands, midslopes, bottomlands)

Acer negundo L.
Acer saccharinum L.
Acer saccharum Marshall
Actaea alba (L.) Miller
Adiantum pedatum L.
Alliara petiolata (Bieb.) Cavara & Grande
Allium tricoccum Aiton
Ambrosia trifida L.
Amphicarpaea bracteata (L.) Fern
Anemone virginiana L.
Anemonella thalictroides (L.) Spach.
Aralia nudicaulis L.
Arisaema triphyllum (L.) Schott
Asarum canadense L.
Athyrium filix-femina (L.) Roth
Botrychium virginianum (L.) Swartz
Cardamine concatenata (Michx.) O.Schwarz
Carex albursina Sheldon
Carex amphibola var. turgida Steudel
Carex blanda Dewey
Carex hirtifolia Mackenzie
Carex jameelia Schwein
Carex oligocarpa Schk.
Carex rosea Schk.
Carya cordiformis (Wangenh.) K. Koch
Carya ovata (Miller) K. Koch
Caulophyllum thalictroides (L.) Michx.
Celtis occidentalis L.
Circeae lutetiana L.

Claytonia virginica L.
Cornus sp. L.
Cryptotaenia canadensis (L.) DC.
Cuscuta gronovii Willd.
Cystopteris protrusa (Weatherby) Blasdell
Daucus carota L.
Desmodium glutinosum (Muhi). A. Wood
Desmodium sp. Desv.
Dicentra canadensis (Goldie) Walp.
Dicentra cucullaria (L.) Bernh
Ellisia nyctelea (L.) L.
Erythronium albidum Nutt.
Eupatorium purpureum L.
Eupatorium rugosum Houtuyn
Festuca subverticillata (Pers.) E. Alexeev
Fraxinus americana L.
Fraxinus sp. L.
Galium aparine L.
Galium asprellum Michx.
Galium triflorum Michx.
Geranium maculatum L.
Geum canadense Jacq.
Glechoma hederacea L.
Hackelia virginiana (L.) 1.M. Johnston
Humulus lupulus L.
Hydrophyllum appendiculatum Michx.
Hydrophyllum virginianum L.
Impatiens sp. L.
Isopyrum bistematum (Raf.) T.&G.
Juglans nigra L.
Laportea canadensis (L.) Wedd.
Menispermum canadense L.
Morus alba L.
Morus sp. L.
Osmorhiza claytonii (Michx.) C.B.Clarke
Osmorhiza longistylis (Torr.) DC.
Osmunda claytoniana L.
Ostrya virginiana (Miller) K.Koch
Panax quinquefolius L.
Parthenocissus quinquefolia (L.) Planchon
Phalaris arundinacea L.
Phlox divaricata L.
Phryma leptostachya L.
Pilea pumila (L.) A.Gray
Poa sylvestris A.Gray
Podophyllum peltatum L.
Polygonum sp. L.
Polygonum virginianum L.
Prunus serotina Ehrh.
Quercus alba L.
Quercus rubra L.
Ranunculus hispidus Michx.
Ranunculus recurvatus Poiret
Ranunculus sp. L.
Ribes missouriense Nutt.
Preserved area 2: Wickiup Hill Natural Area
(uplands, mid slopes, bottomlands)

*Acer negundo* L.
*Acer nigrum* Michx. f.
*Acer saccharinum* L.
*Adiantum pedatum* L.
*Agrimonia pubescens* Wallr.
*Allium tricoccum* Aiton
*Amphicarpaea bracteata* (L.) Fern
*Anemone quinquefolia* L.
*Anemone virginiana* L.
*Anenomella thalictroides* (L.) Spach.
*Arisaema triphyllum* (L.) Schott
*Asarum canadense* L.
*Asplenium platyneuron* (L.) Oakes
*Aster cordifolius* L.
*Aster lateriflorus* (L.) Britton
*Aster sagittifolius* Willd.
*Aster shortii* Lindley
*Athyrium filix-femina* (L.) Roth
*Athyrium thelypteroides* (Michx.) Desv.
*Barbarea vulgaris* R. Br.
*Blephilia hirsuta* (Pursh) Benth.
*Boehmeria cylindrica* (L.) Swartz
*Botrychium dissectum* Spreng.
*Botrychium virginianum* (L.) Swartz
*Campanula americana* L.
*Cardamine concatenata* (Michx.) O.Schwarz
*Carex albursina* Sheldon
*Carex amphibola* var. *turgida* Steudel
*Carex bcla* Dewey
*Carex cephalophora* Muhl.
*Carex conjuncta* F. Boot.
*Carex convoluta* Mackenzie.
*Carex grayi* Carey
*Carex hirtifolia* Mackenzie

Carex hitchcockiana Dewey
Carex jamesii Schwein
Carex oligocarpa Schk.
Carex pensylvanica Lam.
Carex sprengelii Dewey
Carex stipata Muhl.
*Carya cordiformis* (Wangenh.) K. Koch
*Carya lacinosa* (Michx. F.) Loudon
*Carya ovata* (Miller) K. Koch
*Celtis occidentalis* L.
*Chaerophyllum procumbens* (L.) Crantz
*Circaea lutetiana* L.
*Claytonia virginica* L.
*Cornus alternifolia* L. f.
*Cornus racemosa* Lam.
*Cryptotaenia canadensis* (L.) DC.
*Cystopteris bulbifera* (L.) Bernh
*Cystopteris prostrata* (Weatherby) Blasdell
*Desmodium glutinosum* (Muhl). A. Wood
*Dicentra cucullaria* (L.) Bernh
*Dichanthelium sp.* (A.S.Hitchc. & Chase) Gould
*Echinocystis lobata* (Michx.) T.&G.
*Ellisia nyctelea* (L.) L.
*Elymus virginicus* L.
*Equisetum arvense* L.
*Equisetum hyemale* L.
*Equisetum sylvaticum* L.
*Erigeron philadelphicus* L.
*Erythronium albidum* Nutt.
*Euonymus atropurpureus* Jacq.
*Eupatorium rugosum* Houtuyn
*Eupatorium sp.* L.
*Festuca subverticillata* (Pers.) E. Alexeev
*Fragaria sp.* L.
Fraxinus americana L.
Fraxinus pennsylvanica Marshall
Galium aparine L.
Galium concinnum T.&G.
Galium triflorum Michx.
Geranium maculatum L.
Guea canadense Jacq.
Hackelia virginiana (L.) I.M. Johnston
Helianthus giganteus L.
Heliopsis helianthoides (L.) Sweet
Hepatica nobilis var. acuta DC.
Heracleum lanatum Michx.
Hydrophyllum appendiculatum Michx.
Hydrophyllum virginianum L.
Impatiens sp. L.
Isopyrum biternatum (Raf.) T.&G.
Juglans cinerea L.
Juglans nigra L.
Juniperus virginiana L.
Lactuca sp. L.
Laportea canadensis (L.) Wedd.
Leersia virginica Willd.
Lonicera dioica L.
Lysimachia nummularia L.
Mitella diphylia L.
Morus rubra L.
Onoclea sensibilis L.
Osmorhiza claytonii (Michx.) C.B.Clarke
Ostrya virginiana (Miller) K.Koch
Parthenocissus quinquefolia (L.) Planchon
Parthenocissus vitacea (Knerr) A.Hitchc.
Phalaris arundinacea L.
Phlox divaricata L.
Phryma leptostachya L.
Pilea pumila (L.) A.Gray
Plantago rugelii Decne.
Podophyllum peltatum L.
Polygonatum biflorum (Walter) Elliott
Polygonum sp. L.
Polygonum virginianum L.
Populus deltoides Marshall
Populus grandidentata Michx.
Populus sp. L.
Potentilla sp. L.
Prunella vulgaris L.
Prunus serotina Ehrh.
Quercus alba L.
Quercus rubra L.
Ranunculus abortivus L.
Ranunculus fascicularis Muhl.
Ranunculus hispidus Michx.
Ribes sp. L.
Robinia pseudoacacia L.
Rosa multiflora Thunb.
Rosa sp. L.
Rubus sp. L.
Rudbeckia lacinata L.
Salix sp. L.
Sanguinaria canadensis L.
Sanicula gregaria E.Bickn.
Scrophularia marilandica L.
Smilacina racemosa (L.) Desf.
Smilax ecierta (Engeln.) S.Wats.
Smilax herbacea L.
Smilax hispida Muhl.
Solidago canadensis L.
Solidago flexicaulis L.
Solidago ulmifolia Muhl.
Staphylea trifolia L.
Symlocarpus foetidus (L.) Nutt.
Taraxacum officinale Weber ex. Wiggers
Teucrium canadense L.
Tilia americana L.
Toxicodendron radicans (L.) Kuntze
Trifolium hybridum L.
Trillium sp. L.
Ulmus americana L.
Ulmus rubra Muhl.
Urtica dioica L.

Uvularia grandiflora J.E.Smith
Verbena urticaefolia L.
Viola pubescens Aiton
Viola sororia Willd.
Vitis riparia Michx.
Zanthoxylum americanum Miller
Preserved area 3a: Hoefle-Dulin Area
(uplands, midslopes)

*Acer nigrum* Michx. F.
*Actaea alba* (L.) Miller
*Actaea rubra* (Aiton) Willd.
*Actaea sp.* L.
*Adiantum pedatum* L.
*Alliara petiolata* (Bieb.) Cavara & Grande
*Allium tricoccum* Aiton
*Anemone virginiana* L.
*Anemonella thalictroides* (L.) Spach.
*Arisaema triphyllum* (L.) Schott
*Aster cordifolius* L.
*Aster lateriflorus* (L.) Britton
*Aster puniceus* L.
*Aster shortii* Lindley
*Athyrium filix-femina* (L.) Roth
*Botrychium virginianum* (L.) Swartz
*Cardamine concatenata* (Michx.) O.Schwarz
*Carex amphibola* var. *turgida* Steudel
*Carex blanda* Dewey
*Carex cephalophora* Muhl.
*Carex hirtifolia* Mackenzie
*Carex pensylvanica* Lam.
*Carex rosea* Schk.
*Carex sparagnoides* Muhl.
*Carya cordiformis* (Wangenh.) K. Koch
*Carya ovata* (Miller) K. Koch
*Caulophyllum thalictroides* (L.) Michx.
*Celtis occidentalis* L.
*Circaea lutetiana* L.
*Claytonia virginica* L.
*Cornus alternifolia* L. f.
*Cornus sp.* L.
*Cryptotaenia canadensis* (L.) DC.
*Cystopteris bulbifera* (L.) Bernh

*Cystopteris protrusa* (Weatherby) Blasdell
*Daucus carota* L.
*Dicentra cucullaria* (L.) Bernh
*Dioscorea villosa* L.
*Ellisia nyctelea* (L.) L.
*Elymus villosus* Muhl.
*Elymus virginicus* L.
*Erythronium albidum* Nutt.
*Euonymus atropurpureus* Jacq.
*Euonymus sp.* L.
*Festuca subverticillata* (Pers.) E. Alexeev
*Galium aparine* L.
*Galium asprellum* Michx.
*Galium triflorum* Michx.
*Geranium maculatum* L.
*Glechoma hederacea* L.
*Hackelia virginiana* (L.) I.M. Johnston
*Hepatica nobilis* var. *acuta* DC.
*Hydrophyllum virginianum* L.
*Impatiens sp.* L.
*Isopyrum biternatum* (Raf.) T.&G.
*Juglans nigra* L.
*Laportea canadensis* (L.) Wedd.
*Leersia virginica* Willd.
*Lonicera sp.* L.
*Menispermum canadense* L.
*Osmorhiza claytonii* (Michx.) C.B.Clarke
*Ostrya virginiana* (Miller) K.Koch
*Parthenocissus quinquefolia* (L.) Planchon
*Parthenocissus vitacea* (Knerr) A.Hitchc.
*Phalaris arundinaea* L.
*Phlox divaricata* L.
*Phryma leptostachya* L.
*Physalis heterophylla* Nees.
*Pilea pumila* (L.) A.Gray

*Podophyllum peltatum* L.

*Polemonium reptans* L.

*Polygonum virginianum* L.

*Prunus serotina* Ehrh.

*Prunus virginiana* L.

*Quercus alba* L.

*Quercus rubra* L.

*Quercus sp.* L.

*Ranunculus abortivus* L.

*Ranunculus pensylvanicus* L.f.

*Ranunculus recurvatus* Poiret

*Ribes missouriense* Nutt.

*Ribes sp.* L.

*Rosa sp.* L.

*Sambucus canadensis* L.

*Sambucus sp.* L.

*Sanguinaria canadensis* L.

*Sanicula gregaria* E.Bickn.

*Smilacina racemosa* (L.) Desf.

*Smilax ecirrata* (Engelm.) S.Wats.

*Smilax hispida* Muhl.

*Solidago flexicaulis* L.

*Solidago ulmifolia* Muhl.

*Teucrium canadense* L.

*Tilia americana* L.

*Toxicodendron radicans* (L.) Kuntze

*Trillium nivale* Riddell

*Ulmus rubra* Muhl.

*Urtica dioica* L.

*Uvularia grandiflora* J.E.Smith

*Veronicastrum virginicum* (L.) Farw.

*Viola pubescens* Aiton

*Viola sororia* Willd.

*Vitis riparia* Michx.
Preserved area 3b: Dudgeon Lake Area (bottomlands)

Acer negundo L.
Alnus incana (L.) Moench
Aralia racemosa L.
Campanula americana L.
Carex amphibola var. turgida Steudel
Carex grayi Carey
Carex oligocarpa Schk.
Carya cordiformis (Wangenh.) K. Koch
Celtis occidentalis L.
Chaerophyllum procumbens (L.) Crantz
Claytonia virginica L.
Crataegus sp. L.
Elymus virginicus L.
Fraxinus pennsylvanica Marshall
Galium aparine L.
Geum canadense Jacq.
Gleditsia triacanthos L.
Isopyrum biternatum (Raf.) T.&G.
Lactuca floridana (L.) Gaertner
Laportea canadensis (L.) Wedd.
Leonurus cardiaca L.
Morus alba L.
Phalaris arundinacea L.
Physalis heterophylla Nees.
Physostegia virginiana (L.) Benth.
Pilea pumila (L.) A.Gray
Polymnia canadensis L.
Prunella vulgaris L.
Quercus macrocarpa Michx.
Quercus sp. L.
Robinia pseudoacacia L.
Rudbeckia lacinata L.
Smilax ecirrata (Engelm.) S.Wats.
Smilax hispida Muhl.
Solanum sp. L.
Taraxacum officinale Weber ex. Wiggers
Toxicodendron radicans (L.) Kuntze
Ulmus rubra Muhl.
Urtica dioica L.
Viola sororia Willd.
Viola sp. L.
Vitis riparia Michx.
Managed area 1: Engelken
(uplands, midslopes, bottomlands)
Acer negundo L.
Acer nigrum Michx. f.
Actaea rubra (Aiton) Willd.
Actaea sp. L.
Adiantum pedatum L.
Agrimonia pubescens Wallr.
Allium tricoccum Aiton
Amphicarpaea bracteata (L.) Fern
Aplectrum hyemale (Muhl.) Torr.
Aquilegia canadensis L.
Aralia nudicaulis L.
Arisaema triphyllum (L.) Schott
Aster lateriflorus (L.) Britton
Athyrium filix-femina (L.) Roth
Berberis vulgaris L.
Blephilia hirsuta (Pursh) Benth.
Botrychium virginianum (L.) Swartz
Campanula americana L.
Carex amphibola var. turgida Steudel
Carex blanda Dewey
Carex cf. retroflexa Muhl.
Carex convoluta Mackenzie
Carex hirtifolia Mackenzie
Carex hitchcockiana Dewey
Carex jamesii Schwein
Carex sparagnoides Muhl.
Carya cordiformis (Wangenh.) K. Koch
Caulophyllum thalictroides (L.) Michx.
Celtis occidentalis L.
Chenopodium album L.
Circaea lutetiana L.
Claytonia virginica L.
Cornus alternifolia L. f.
Cornus racemosa Lam.
Cryptotaenia canadensis (L.) DC.
Cuscuta sp. L.
Cystopteris bulbifera (L.) Bernh
Cystopteris prostrusa (Weatherby) Blasdel
Desmodium glutinorum (Muhl). A. Wood
Dien延a cucullaria (L.) Bernh
Dioscorea villosa L.
Dryopteris carthusiana (Villars) H.P. Fuchs
Elymus hystrix L.
Equisetum arvense L.
Eupatorium maculatum L.
Eupatorium purpureum L.
Eupatorium rugosum Houtuyn
Festuca subverticillata (Pers.) E. Alexeev
Fraxinus americana L.
Fraxinus pennsylvanica Marshall
Galearis spectabilis L.
Galium aparine L.
Galium circaeans Michx.
Galium concinnum T.&G.
Galium triflorum Michx.
Geranium maculatum L.
Geum canadense Jacq.
Hamamelis virginiana L.
Helianthus decapetalus L.
Hydrophyllum virginianum L.
Impatiens capensis Meerb.
Impatiens sp. L.
Ipomoea coccinea L.
Ipomoea sp. L.
Isopyrum biternatum (Raf.) T.&G.
Juglans nigra L.
Laportea canadensis (L.) Wedd.
Lonicera sp. L.
Menispermum canadense L.
Monarda fistulosa L.
Onoclea sensibilis L.
Osmorhiza claytonii (Michx.) C.B.Clarke
Osmorhiza longistyliis (Torr.) DC.
Ostrya virginiana (Miller) K.Koch
Oxalis stricta L.
Panax quinquefolius L.
Parthenocissus quinquefolia (L.) Planchon
Parthenocissus vitacea (Knerr) A.Hitchc.
Phlox divaricata L.
Phryma leptostachya L.
Pilea pumila (L.) A.Gray
Plantago rugelii Decne.
Podophyllum peltatum L.
Polemonium reptans L.
Polygonatum biflorum (Walter) Elliott
Polygonum virginianum L.
Polymnia canadensis L.
Populus tremuloides Michx.
Prenanthes alba L.
Prunus serotina Ehrh.
Prunus virginiana L.
Quercus alba L.
Quercus rubra L.
Ranunculus abortivus L.
Rhamnus sp. L.
Ribes sp. L.
Robinia pseudoacacia L.
Rosa multiflora Thunb.
Rosa sp. L.
Rubus allegheniensis T.C.Porter
Rubus sp. L.
Sambucus canadensis L.
Sanguinaria canadensis L.
Sanicula gregaria E.Bickn.
Sanicula marilandica L.
Sanicula trifoliata E.Bickn.
Scirpus atrovirens Willd.
Scrophularia marilandica L.
Smilacina racemosa (L.) Desf.
Smilax ecirrata (Engelm.) S.Wats.
Smilax herbacea L.
Smilax hispida Muhl.
Solanum americanum P.Miller
Solidago flexicaulis L.
Solidago ulmifolia Muhl.
Teucrium canadense L.
Thalictrum dioicum L.
Tilia americana L.
Toxicodendron radicans (L.) Kuntze
Triosteum perfoliatum L.
Triphora trianthophora (Swartz) Rydb.
Ulmus rubra Muhl.
Ulmus sp. L.
Urtica dioica L.
Uvularia grandiflora J.E.Smith
Viola pubescens Aiton
Vitis riparia Michx.
Zanthoxylum americanum Miller
Zizia aurea (L.) Koch
Managed area 2a: Steintjes
(uplands, mid-slopes)

_Acer negundo_ L.
_Acer nigrum_ Michx. f.
_Actaea alba_ (L.) Miller
_Adiantum pedatum_ L.
_Agrimonia pubescens_ Wallr.
_Alliara petiolata_ (Bieb.) Cavara & Grande
_Amphicarpaea bracteata_ (L.) Fern
_Annenomella thalictroides_ (L.) Spach.
_Arabis hirsuta_ (L.) Scop.
_Aralia triphylla_ (L.) Schott
_Aster cordifolius_ L.
_Aster lateriflorus_ (L.) Britton
_Aster shortii_ Lindley
_Athyrium filix-femina_ (L.) Roth
_Athyrium thelypteroides_ (Michx.) Desv.
_Berberis vulgaris_ L.
_Botrychium multifidum_ (S.G.Gmelin) Rupr.
_Botrychium virginianum_ (L.) Swartz
_Carex amphibola_ var. _turgida_ Steudel
_Carex blanda_ Dewey
_Carex hirtifolia_ Mackenzie
_Carex jamesii_ Schwein
_Carex pensylvanica_ Lam.
_Carya cordiformis_ (Wangenh.) K. Koch
_Carya ovata_ (Miller) K. Koch
_Caulophyllum thalictroides_ (L.) Michx.
_Celts occidentalis_ L.
_Chaerophyllum procumbens_ (L.) Crantz
_Circaea lutetiana_ L.
_Claytonia virginica_ L.
_Cornus amomum_ Miller
_Cornus racemosa_ Lam.
_Cornus sericea_ L.

_Cryptotaenia canadensis_ (L.) DC.
_Cystopteris protrusa_ (Weatherby) Blasdel
_Desmodium canadense_ (L.) DC.
_Desmodium glutinosum_ (Muhl.) A. Wood
_Desmodium nudiflorum_ (L.) DC.
_Dichanthelium latifolium_ (L.) Harrill
_Dioscorea villosa_ L.
_Euonymus atropurpureus_ Jacq.
_Eupatorium rugosum_ Houtyyn
_Festuca subverticillata_ (Pers.) E. Alexeev
_Fraxinus americana_ L.
_Fraxinus pennsylvanica_ Marshall
_Galium aparine_ L.
_Galium concinnum_ T&G.
_Galium triflorum_ Michx.
_Geranium maculatum_ L.
_Geum canadense_ Jacq.
_Gleditsia triacanthos_ L.
_Goodyera pubescens_ (Willd.) R. Br.
_Hackelia virginiana_ (L.) I.M. Johnston
_Hamamelis virginiana_ L.
_Helianthus decapetalus_ L.
_Hepatica nobilis_ var. _acuta_ DC.
_Hydrophyllum virginianum_ L.
_Impatiens sp._ L.
_Juglans nigra_ L.
_Laportea canadensis_ (L.) Wedd.
_Lonicera japonica_ Thunb.
_Lonicera tatarica_ L.
_Menispernum canadense_ L.
_Mitella diphylla_ L.
_Osmorhiza claytonii_ (Michx.) C.B.Clarke
_Osmorhiza longistylos_ (Torr.) DC.
_Ostrya virginiana_ (Miller) K.Koch
Oxalis stricta L.
Parthenocissus quinquefolia (L.) Planchon
Parthenocissus vitacea (Knerr) A. Hitchc.
Phryma leptostachya L.
Pilea pumila (L.) A. Gray
Plantago major L.
Plantago rugelii Decne.
Podophyllum peltatum L.
Polemonium reptans L.
Polygonatum biflorum (Walter) Elliott
Polygonum virginianum L.
Polymnia canadensis L.
Potentilla sp. L.
Prunus serotina Ehrh.
Prunus virginiana L.
Quercus alba L.
Quercus rubra L.
Ranunculus abortivus L.
Rhamnus cathartica L.
Ribes sp. L.
Rosa sp. L.
Rubus allegheniensis T.C. Porter
Rubus sp. L.
Sambucus canadensis L.
Sambucus sp. L.
Sanguinaria canadensis L.
Sanicula gregaria E. Bickn.
Sanicula marilandica L.
Smilacina racemosa (L.) Desf.
Smilax ecirrata (Engelm.) S. Wats.
Smilax herbacea L.
Smilax hispida Muhl.
Solidago flexicaulis L.
Solidago ulmifolia Muhl.
Staphylea trifolia L.
Taraxacum officinale Weber ex. Wiggers
Teucrium canadense L.
Tilia americana L.
Toxicodendron radicans (L.) Kuntze
Triosteum perfoliatum L.
Ulmus americana L.
Ulmus rubra Muhl.
Uvularia grandiflora J. E. Smith
Veronicastrum virginicum (L.) Farw.
Viburnum acerifolium L.
Viola pubescens Aiton
Viola sororia Willd.
Viola striata Aiton
Vitis riparia Michx.
Managed area 2b: Neitert & Pienkos
(bottonlands)

_Arisaema dracontium_ (L.) Schott
_Celtis occidentalis_ L.
_Cornus racemosa_ Lam.
_Cryptotaenia canadensis_ (L.) DC.
_Equisetum arvense_ L.
_Pilea pumila_ (L.) A.Gray
_Polygonum virginianum_ L.
_Populus deltoides_ Marshall
_Quercus bicolor_ Willd.
_Ranunculus abortivus_ L.
_Ranunculus hispidus_ Michx.
_Rosa sp._ L.

_Rudbeckia lacinata_ L.
_Sambucus canadensis_ L.
_Smilax herbacea_ L.
_Smilax hispida_ Muhl.
_Teucrium canadense_ L.
_Toxicodendron radicans_ (L.) Kuntze
_Ulmus sp._ L.
_Ulmus thomasii_ Sarg.
_Urtica dioica_ L.
_Viola sp._ L.
_Vitis riparia_ Michx.
Managed area 3a: Jordan & Vislisl
(uplands, midslopes)
Acer negundo L.
Acer nigrum Michx. f.
Acer saccharum Marshall
Agrimonia pubescens Wallr.
Alliara petiolata (Bieb.) Cavara & Grande
Allium tricoccum Aiton
Ambrosia trifida L.
Amphicarpaea bracteata (L.) Fern
Arabis hirsuta (L.) Scop.
Aralia nudicaulis L.
Arisaema triphyllum (L.) Schott
Aster cordifolius L.
Aster lateriflorus (L.) Britton
Aster sagittifolius Willd.
Aster shortii Lindley
Athyrium filix-femina (L.) Roth
Botrychium multifidum (S.G.Gmelin) Rupr.
Botrychium virginianum (L.) Swartz
Campanula americana L.
Cardamine concatenata (Michx.) O.Schwarz
Carex albursina Sheldon
Carex amphibola var. turgida Steudel
Carex blanda Dewey
Carex davisii Schwein & Torr.
Carex hirtifolia Mackenzie
Carex hitchcockiana Dewey
Carex jameissii Schwein
Carex pensylvanica Lam.
Carex rosea Schk.
Carya cordiformis (Wangenh.) K. Koch
Carya ovata (Miller) K. Koch
Caulophyllum thalictroides (L.) Michx.
 Celtis occidentalis L.
 Circaea lutetiana L.

Claytonia virginica L.
Cornus sp. L.
Cryptotaenia canadensis (L.) DC.
Cystopteris protrusa (Weatherby) Blasdel
Desmodium glutinosum (Muhl). A. Wood
Desmodium sp. Desv.
Dicentra cucullaria (L.) Bernh
Dioscorea villosa L.
Elymus virginicus L.
Eupatorium purpureum L.
Eupatorium rugosum Houttyna
Festuca subverticillata (Pers.) E. Alexeev
Fraxinus americana L.
Galium aparine L.
Galium boreale L.
Galium sp. L.
Galium triflorum Michx.
Geranium maculatum L.
Geum canadense Jacq.
Glechoma hederacea L.
Hackelia virginiana (L.) I.M. Johnston
Humulus lupulus L.
Hydrophyllum appendiculatum Michx.
Hydrophyllum virginianum L.
Impatiens pallida Nutt.
Impatiens sp. L.
Ipomoea sp. L.
Juglans nigra L.
Laportea canadensis (L.) Wedd.
Leersia virginica Willd.
Menispermum canadense L.
Osmorhiza claytonii (Michx.) C.B.Clarke
Osmorhiza longistylis (Torr.) DC.
Ostrya virginiana (Miller) K.Koch
Parthenocissus quinquefolia (L.) Planchon
Parthenocissus vitacea (Knerr) A.Hitchc.
Phlox divaricata L.
Phryma leptostachya L.
Pilea pumila (L.) A.Gray
Plantago major L.
Poa sylvestris A.Gray
Podophyllum peltatum L.
Polygonatum biflorum (Walter) Elliott
Polygonum scandens L.
Polygonum virginianum L.
Polymnia canadensis L.
Prunus serotina Ehrh.
Prunus sp. L.
Quercus rubra L.
Ranunculus abortivus L.
Ribes hirtellum Michx.
Ribes sp. L.
Rosa sp. L.
Rubus sp. L.
Rudbeckia lacinata L.
Sambucus sp. L.
Sanguinaria canadensis L.
Sanicula gregaria E.Bickn.
Sanicula trifoliata E.Bickn.
Smilacina racemosa (L.) Desf.
Smilax ecirrata (Engelm.) S.Wats.
Smilax hispida Muhl.
Solanum americanum P.Miller
Solidago flexicaulis L.
Solidago ulmifolia Muhl.
Tilia americana L.
Toxicodendron radicans (L.) Kuntze
Trillium recurvatum Beck.
Triphora trianthophora (Swartz) Rydb.
Ulmus rubra Muhl.
Ulmus sp. L.
Ulmus thomasii Sarg.
Urtica dioica L.
Uvularia grandiflora J.E.Smith
Viola pubescens Aiton
Viola sororia Willd.
Managed area 3b: Duello
(bottom/ands)

Ambrosia trifida L.
Aster lateriflorus (L.) Britton
Bidens frondosa L.
Campanula americana L.
Carex amphibola var. turgida Steudel
Carex grayi Carey
Carex jamesii Schwein
Celtis occidentalis L.
Chaerophyllum procumbens (L.) Crantz
Chenopodium album L.
Cryptotaenia canadensis (L.) DC.
Cuscuta gronovii Willd.
Elymus virginicus L.
Fraxinus pennsylvanica Marshall
Galium aparine L.
Geum canadense Jacq.
Gleditsia triacanthos L.
Hackelia virginiana (L.) I.M. Johnston
Ipomoea sp. L.
Laportea canadensis (L.) Wedd.
Leersia virginica Willd.
Liatris sp. Schreb.
Menispermum canadense L.

Phalaris arundinacea L.
Physalis heterophylla Nees.
Physostegia virginiana (L.) Benth.
Pilea pumila (L.) A.Gray
Polygonum hydropiper L.
Polygonum persicaria L.
Potentilla norvegica L.
Rudbeckia lacinata L.
Scrophularia marilandica L.
Sicyos angulatus L.
Smilax hispida Muhl.
Solidago canadensis L.
Stachys tenuifolia Willd.
Stellaria aquatica (L.) Scop.
Symlocarpus foetidus (L.) Nutt.
Taraxacum officinale Weber ex. Wiggers
Teucrium canadense L.
Toxicodendron radicans (L.) Kuntze
Ulmus rubra Muhl.
Urtica dioica L.
Viola sororia Willd.
Vitis riparia Michx.
Developed area 1a: Beaver Hollow
(midslopes)

Acer negundo L.
Acer nigrum Michx. f.
Actaea alba (L.) Miller
Agrimonia alba (L.) Miller
Agrimonia pubescens Wallr.
Agrimonia sp. L.
Alliaria petiolata (Bieb.) Cavara & Grande
Amphicarpaea bracteata (L.) Fern
Anemone sp. L.
Anenomella thalictroides (L.) Spach.
Apocynum sp. L.
Aralia nudicaulis L.
Arisaema triphyllum (L.) Schott
Aster lateriflorus (L.) Britton
Athyrium filix-femina (L.) Roth
Berberis vulgaris L.
Campanula americana L.
Carex cephalophora Muhl.
Carex convoluta Mackenzie
Carex hirtifolia Mackenzie
Carex oligocarpa Schk.
Carex rosea Schk.
Carpinus caroliniana Walter
Carya cordiformis (Wangenh.) K. Koch
Carya ovata (Miller) K. Koch
Carya sp. Nutt.
Celtis occidentalis L.
Chenopodium album L.
Cinna arundinacea L.
Circaea lutetiana L.
Claytonia virginica L.
Cornus drummondii C.A. Meyer
Cornus sp. L.
Cratageus sp. L.

Cryptotaenia canadensis (L.) DC.
Cystopteris protrusa (Weatherby) Blasdell
Cystopteris protrusa (Weatherby) Blasdell
Desmodium canadense (L.) DC.
Desmodium glutinosum (Muhl). A. Wood
Desmodium nudiflorum (L.) DC.
Dichanthelium sp. (A.S. Hitchc. & Chase) Gould
Dioscorea villosa L.
Eupatorium rugosum Houtyyn
Festuca subverticillata (Pers.) E. Alexeev
Fraxinus americana L.
Fraxinus pennsylvanica Marshall
Galium aparine L.
Galium asprellum Michx.
Galium concinnum T.&G.
Galium triflorum Michx.
Geranium maculatum L.
Geum canadense Jacq.
Hackelia virginiana (L.) I.M. Johnston
Hamamelis virginiana L.
Hepatica nobilis var. acuta DC.
Hydrophyllum virginianum L.
Juglans cinerea L.
Juncus cf. tenuis Willd.
Laportea canadensis (L.) Wedd.
Leersia virginica Willd.
Lonicera sp. L.
Lonicera tatarica L.
Menispermum canadense L.
Onoclea sensibilis L.
Osmorhiza claytonii (Michx.) C.B.Clarke
Osmorhiza sp. Raf.
Osmunda claytoniana L.
Ostrya virginiana (Miller) K. Koch
Oxalis stricta L.
Parthenocissus quinquefolia (L.) Planchon
Parthenocissus vitacea (Knerr) A.Hitchc.
Phlox divaricata L.
Phryma leptostachya L.
Phytolacca americana L.
Pilea pumila (L.) A.Gray
Podophyllum peltatum L.
Polemonium reptans L.
Polygonatum biflorum (Walter) Elliott
Polygonum scandens L.
Polygonum sp. L.
Polygonum virginianum L.
Polymnia canadensis L.
Populus tremuloides Michx.
Potentilla recta L.
Prunella vulgaris L.
Prunus pensylvanica L.f.
Prunus serotina Ehrh.
Quercus alba L.
Quercus rubra L.
Ranunculus abortivus L.
Ribes sp. L.
Robinia pseudoacacia L.
Rosa sp. L.
Rubus sp. L.
Sanguinaria canadensis L.
Sanicula canadensis L.
Sanicula gregaria E.Bickn.
Sanicula marilandica L.
Smilax ecirrata (Engelm.) S.Wats.
Smilax hispida Muhl.
Solidago flexicaulis L.
Solidago ulmifolia Muhl.
Teucrium canadense L.
Tilia americana L.
Toxicodendron radicans (L.) Kuntze
Trillium recurvatum Beck.
Triosteum perfoliatum L.
Ulmus americana L.
Ulmus rubra Muhl.
Uvularia grandiflora J.E.Smith
Veronicastrum virginicum (L.) Farw.
Viburnum acerifolium L.
Viola pubescens Aiton
Viola sororia Willd.
Vitis riparia Michx.
Developed area 1b: River Ridge
(uplands)

Acer negundo L.
Acer nigrum Michx. f.
Actaea alba (L.) Miller
Agrimonia pubescens Wallr.
Alliara petiolata (Bieb.) Cavara & Grande
Anemomella thalictroides (L.) Spach.
Apocynum sp. L.
Arisaema triphyllum (L.) Schott
Athyrium filix-femina (L.) Roth
Berberis vulgaris L.
Carex cephalophora Muhl.
Carex convoluta Mackenzie
Carex hirtifolia Mackenzie
Carex oligocarpa Schk.
Carex rosea Schk.
Carya ovata (Miller) K. Koch
Carya sp. Nutt.
Celtis occidentalis L.
Chenopodium album L.
Circaea lutetiana L.
Cornus drummondii C.A. Meyer
Crataegus sp. L.
Desmodium canadense (L.) DC.
Desmodium glutinosum (Muhl). A. Wood
Desmodium nudiflorum (L.) DC.
Dichanthelium sp. (A.S.Hitchc. & Chase) Gould
Eupatorium rugosum Houtuyn
Festuca subverticillata (Pers.) E. Alexeev
Fraxinus americana L.
Galium aparine L.
Galium concinnum T.&G.
Galium triflorum Michx.

Hackelia virginiana (L.) I.M. Johnston
Hamamelis virginiana L.
Juglans cinerea L.
Leersia virginica Willd.
Lonicera tatarica L.
Menispermum canadense L.
Osmorrhiza sp. Raf.
Ostrya virginiana (Miller) K.Koch
Oxalis stricta L.
Parthenocissus quinquefolia (L.) Planchon
Podophyllum peltatum L.
Polygonatum biflorum (Walter) Elliott
Polygonum scandens L.
Polygonum virginianum L.
Polymnia canadensis L.
Populus tremuloides Michx.
Prunus pensylvanica L.f.
Prunus serotina Ehrh.
Quercus alba L.
Quercus rubra L.
Ribes sp. L.
Robinia pseudoacacia L.
Rosa sp. L.
Rubus sp. L.
Smilax ecirrata (Engelm.) S.Wats.
Smilax hispida Muhl.
Solidago ulmifolia Muhl.
Teucrium canadense L.
Tilia americana L.
Triosteum perfoliatum L.
Ulmus americana L.
Viola sororia Willd.
Vitis riparia Michx.
Developed area 2: Oak Woods
(uplands, midslopes)

Acer negundo L.
Acer nigrum Michx. f.
Adiantum pedatum L.
Agrimonia sp. L.
Alliara petiolata (Bieb.) Cavara & Grande
Amelanchier arborea (Michx. f.) Fern
Anemone sp. L.
Anenomella thalictroides (L.) Spach.
Aralia racemosa L.
Arisaema triphyllum (L.) Schott
Aster lateriflorus (L.) Britton
Athyrium filix-femina (L.) Roth
Botrychium virginianum (L.) Swartz
Carex convoluta Mackenzie
Carex hirtifolia Mackenzie
Carex pensylvanica Lam.
Carya cordiformis (Wangenh.) K. Koch
Carya ovata (Miller) K. Koch
Caulophyllum thalictroides (L.) Michx.
Celtis occidentalis L.
Chenopodium album L.
Circaea lutetiana L.
Claytonia virginica L.
Cornus alternifolia L. f.
Cornus sp. L.
Crataegus sp. L.
Cryptotaenia canadensis (L.) DC.
Cystopteris protonema (Weatherby) Blasdell
Desmodium glutinosum (Muhl). A. Wood
Desmodium sp. Desv.
Dioscorea villosa L.
Eupatorium rugosum Houttuyn
Fraxinus americana L.
Fraxinus pennsylvanica Marshall
Galearis spectabilis L.

Galium aparine L.
Galium asprellum Michx.
Galium concinnum T.&G.
Galium triflorum Michx.
Geranium maculatum L.
Geum canadense Jacq.
Gleditsia triacanthos L.
Hackelia virginiana (L.) I.M. Johnston
Hamamelis virginiana L.
Leersia virginica Wild.
Lonicera japonica Thunb.
Menispermum canadense L.
Onoclea sensibilis L.
Osmorhiza claytonii (Michx.) C.B.Clarke
Osmunda claytoniana L.
Oxalis stricta L.
Parthenocissus quinquefolia (L.) Planchon
Parthenocissus vitacea (Knerr) A.Hitchc.
Phalaris arundinacea L.
Phryma leptostachya L.
Pilea pumila (L.) A.Gray
Podophyllum peltatum L.
Polemonium reptans L.
Polygonum hydropiper L.
Polygonum scandens L.
Polygonum virginianum L.
Prunus serotina Ehrh.
Quercus alba L.
Quercus rubra L.
Rhamnus sp. L.
Ribes sp. L.
Rosa sp. L.
Rubus sp. L.
Sambucus sp. L.
Sanicula gregaria E.Bickn.
Smilax hispida Muhl.
Solanum americanum P.Miller
Teucrium canadense L.
Tilia americana L.
Toxicodendron radicans (L.) Kuntze
Ulmus americana L.

Ulmus rubra Muhl.
Urtica dioica L.
Uvularia grandiflora J.E.Smith
Viola pubescens Aiton
Viola sororia Willd.
Vitis riparia Michx.
Developed area 3: Riverbend
(uplands, midslopes)

Acer negundo L.
Acer nigrum Michx. f.
Acer sp. L.
Agrimonia pubescens Wallr.
Agrimonia sp. L.
Alliara petiolata (Bieb.) Cavara & Grande
Allium tricoccum Aiton
Amphicarpaea bracteata (L.) Fern
Anemone quinquefolia L.
Anenomella thalictroides (L.) Spach.
Aralia racemosa L.
Arisaema dracontium (L.) Schott
Arisaema triphyllum (L.) Schott
Aster lateriflorus (L.) Britton
Aster sp. L.
Athyrium filix-femina (L.) Roth
Botrychium virginianum (L.) Swartz
Carex amphibola var. turgida Steudel
Carex blanda Dewey
Carex convoluta Mackenzie
Carex hirtifolia Mackenzie
Carex hitchcockiana Dewey
Carex pensylvanica Lam.
Carex rosea Schk.
Carya cordiformis (Wangenh.) K. Koch
Carya ovata (Miller) K. Koch
Celtis occidentalis L.
Chaerophyllum procumbens (L.) Crantz
Chenopodium album L.
Circaea lutetiana L.
Claytonia virginica L.
Cornus sp. L.
Cratageus sp. L.
Cryptotaenia canadensis (L.) DC.
Cystopteris protrusa (Weatherby) Blasdel

Daucus carota L.
Desmodium canadense (L.) DC.
Desmodium glutinosum (Muhl.) A. Wood
Dicentra cucullaria (L.) Bernh
Dichanthelium sp. (A.S.Hitchc. & Chase) Gould
Dioscorea villosa L.
Dryopteris carthusiana (Villars) H.P. Fuchs
Ellisia nyctelea (L.) L.
Eupatorium rugosum Houtuy
Festuca subverticillata (Pers.) E. Alexeev
Fraxinus americana L.
Fraxinus pennsylvanica Marshall
Galearis spectabilis L.
Galium aparine L.
Galium concinnum T.&G.
Galium triflorum Michx.
Geranium maculatum L.
Geum canadense Jacq.
Gleditsia triacanthos L.
Hackelia virginiana (L.) I.M. Johnston
Hamamelis virginiana L.
Helianthus sp. L.
Impatiens sp. L.
Isopyrum biternatum (Raf.) T.&G.
Juglans nigra L.
Laportea canadensis (L.) Wedd.
Leersia virginica Willd.
Lonicera sp. L.
Menispermum canadense L.
Moehringia lateriflora L.
Osmorhiza claytonii (Michx.) C.B.Clarke
Osmorhiza longistylis (Torr.) DC.
Osmorhiza sp. Raf.
Ostrya virginiana (Miller) K.Koch
Oxalis stricta L.
Parthenocissus quinquefolia (L.) Planchon
Parthenocissus vitacea (Knerr) A.Hitchc.
Phlox divaricata L.
Phryma leptostachya L.
Pilea pumila (L.) A.Gray
Podophyllum peltatum L.
Polemonium reptans L.
Polygonatum biflorum (Walter) Elliott
Polygonum sp. L.
Polygonum virginianum L.
Polymnia canadensis L.
Potentilla simplex Michx.
Potentilla sp. L.
Prunus serotina Ehrh.
Prunus virginiana L.
Quercus alba L.
Quercus rubra L.
Ranunculus abortivus L.
Ranunculus hispidus Michx.
Ribes sp. L.
Robinia pseudoacacia L.
Rosa sp. L.
Rubus sp. L.
Sanicula canadensis L.
Sanicula gregaria E.Bickn.
Sanicula trifoliata E.Bickn.
Smilacina sp. Desf.
Smilax ecirrata (Engelm.) S.Wats.
Smilax hispida Muhl.
Solidago canadensis L.
Solidago ulmifolia Muhl.
Tilia americana L.
Toxicodendron radicans (L.) Kuntze
Triosteum perfoliatum L.
Ulmus americana L.
Ulmus rubra Muhl.
Urtica dioica L.
APPENDIX B: SPECIES LISTS FOR NUTRIENT SEQUESTRATION BY THE HERBACEOUS LAYER IN DISTURBED AND INTACT HARDWOOD FORESTS IN CENTRAL IOWA, USA

Woodland 1: Conard Environmental Research Area, Jasper County, IA

Intact

Anenomella thalictroides (L.) Spach.
Athyrium filix-femina (L.) Roth
Cardamine concatenata (Michx.) O.Schwarz
Carex blanda Dewey
Carex hirtifolia Mackenzie
Carex pensylvanica Lam.
Circaea lutetiana L.
Claytonia virginica L.
Cryptotaenia canadensis (L.) DC.
Dicentra cucullaria (L.) Bernh
Ellisia nyctelea (L.) L.
Erythronium albidum Nutt.
Eupatorium rugosum Houtuyn
Galium triflorum Michx.
Geranium maculatum L.
Hackelia virginiana (L.) I.M. Johnston
Hydrophyllum virginianum L.
Impatiens sp. L.
Laportea canadensis (L.) Wedd.
Osmorhiza longistylis (Torr.) DC.
Phryma leptostachya L.
Pilea pumila (L.) A.Gray
Podophyllum peltatum L.
Polemonium reptans L.
Polygonatum biflorum (Walter) Elliott
Polygonum virginianum L.
Sanguinaria canadensis L.
Sanicula gregaria E.Bickn.
Smilax sp. L.
Urtica dioica L.
Viola pubescens Aiton
Viola sororia Willd.

Disturbed

Agrimonia gyrosepala Wallr.
Agrimonia pubescens Wallr.
Arctium minus Schk.
Aster cordifolius L.
Aster ontarionis Wieg.
Barbarea vulgaris R. Br.
Botrychium virginianum (L.) Swartz
Campanula americana L.
Carex blanda Dewey
Carex sparganioides Muhl.
Circaea lutetiana L.
Cryptotaenia canadensis (L.) DC.
Ellisia nyctelea (L.) L.
Elymus hystrix L.
Elymus sp. L.
Eupatorium rugosum Houtuyn
Festuca subverticillata (Pers.) E. Alexeev
Galearis spectabilis L.
Galium aparine L.
Galium concinnum T.&G.
Geum canadense Jacq.
Hackelia virginiana (L.) I.M. Johnston
Leersia virginica Willd.
Muhlenbergia sp. Schreber.
Osmorhiza longistylis (Torr.) DC.
Phryma leptostachya L.
Podophyllum peltatum L.
Polygonatum biflorum (Walter) Elliott
Polygonum virginianum L.
Ranunculus abortivus L.
Sanguinaria canadensis L.
Sanicula gregaria E.Bickn.
Silene stellata (L.) Aiton f.
**Smilax ecirrata** (Engelm.) S.Wats.

**Solidago ulmifolia** Muhl.

**Taraxacum officinale** Weber ex. Wiggers

**Viola pubescens** Aiton

Woodland 2: Robison Wildlife Acres, Story County, IA

**Intact**

- *Agastache neptoides* (L.) Kuntze
- *Allium tricoccum* Aiton
- *Asarum canadense* L.
- *Aster cordifolius* L.
- *Cardamine concatenata* (Michx.) O.Schwarz
- *Carex blanda* Dewey
- *Carex pensylvanica* Lam.
- *Claytonia virginica* L.
- *Cryptotaenia canadensis* (L.) DC.
- *Dicentra cucullaria* (L.) Bernh
- *Festuca subverticillata* (Pers.) E. Alexeev
- *Geum canadense* Jacq.
- *Goodyera pubescens* (Wild.) R. Br.
- *Hepatica nobilis* var. acuta DC.
- *Hydrophyllum virginianum* L.
- *Osmorhiza claytonii* (Michx.) C.B.Clarke
- *Oxalis stricta* L.
- *Phlox divaricata* L.
- *Polygonatum biflorum* (Walter) Elliott
- *Ranunculus abortivus* L.
- *Sanguinaria canadensis* L.
- **Smilax ecirrata** (Engelm.) S.Wats.
- *Viola pubescens* Aiton

**Disturbed**

- *Agrimonia pubescens* Wallr.
- *Athyrium filix-femina* (L.) Roth
- *Carex blanda* Dewey
- *Carex pensylvanica* Lam.
- *Carex rosea* Schk.
- *Circaea lutetiana* L.
- *Claytonia virginica* L.
- *Cryptotaenia canadensis* (L.) DC.
- *Dicentra cucullaria* (L.) Bernh
- *Dioscorea villosa* L.
- *Eupatorium rugosum* Houtuyn
- *Galearis spectabilis* L.
- *Galium aparine* L.
- *Galium triflorum* Michx.
- *Impatiens sp.* L.
- *Laportea canadensis* (L.) Wedd.
- *Osmorhiza sp.* Raf.
- *Phlox divaricata* L.
- *Phryma leptostachya* L.
- *Podophyllum peltatum* L.
- *Polygonatum biflorum* (Walter) Elliott
- *Polygonatum pubescens* (Willd.) Pursh
- *Polygonum virginianum* L.
- *Ranunculus abortivus* L.
- *Sanguinaria canadensis* L.
- *Sanicula gregaria* E.Bickn.
- **Smilax ecirrata** (Engelm.) S.Wats.
- *Urtica dioica* L.
- *Viola pubescens* Aiton
Woodland 3: A privately owned parcel near Ames, Story County, IA

Intact

- Allium tricoccum Aiton
- Asarum canadense L.
- Aster sp. L.
- Campanula americana L.
- Carex blanda Dewey
- Carex jamesii Schwein
- Cryptotaenia canadensis (L.) DC.
- Ellisia nyctelea (L.) L.
- Elymus hystrix L.
- Elymus sp. L.
- Galium aparine L.
- Hepatica nobilis var. acuta DC.
- Hydrophyllum virginianum L.
- Isopyrum biternatum (Raf.) T.&G.
- Osmorhiza longistylis (Torr.) DC.
- Phryma leptostachya L.
- Podophyllum peltatum L.
- Polygonatum biflorum (Walter) Elliott
- Ranunculus abortivus L.
- Sanguinaria canadensis L.
- Sanicula gregaria E.Bickn.
- Silphium perfoliatum L.
- Taraxacum officinale Weber ex. Wiggers
- Viola pubescens Aiton

Disturbed

- Agastache neptoides (L.) Kuntze
- Asarum canadense L.
- Bromus sp. L.
- Campanula americana L.
- Carex amphibia var. turgida Steudel
- Carex blanda Dewey
- Circaea lutetiana L.
- Cryptotaenia canadensis (L.) DC.
- Ellisia nyctelea (L.) L.
- Elymus cf. virginicus L.
- Elymus hystrix L.
- Eupatorium purpureum L.
- Eupatorium rugosum Houtuyn
- Galium aparine L.
- Hackelia virginiana (L.) I.M. Johnston
- Laportea canadensis (L.) Wedd.
- Leersia virginica Willd.
- Osmorhiza longistylica (Torr.) DC.
- Phalaris arundinacea L.
- Phlox divaricata L.
- Phryma leptostachya L.
- Plantago major L.
- Polygonatum biflorum (Walter) Elliott
- Ranunculus abortivus L.
- Sanguinaria canadensis L.