

**Oak forest decline and effects of two invasive shrubs  
in the Midwest Driftless Area:  
current status and implications for the future**

by

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To my loving wife Larissa, beautiful son Brandon, and faithful dog Tugen:  
may we never run out of new forests to explore!

## TABLE OF CONTENTS

LIST OF TABLES	v
LIST OF FIGURES	vi
ACKNOWLEDGEMENTS	viii
CHAPTER 1. GENERAL INTRODUCTION	1
INTRODUCTION	1
THESIS ORGANIZATION	3
LITERATURE CITED	3
CHAPTER 2. OAK FOREST DECLINE AND EFFECTS OF TWO INVASIVE SHRUBS IN THE MIDWEST DRIFTLESS AREA: CURRENT STATUS AND IMPLICATIONS FOR THE FUTURE	5
ABSTRACT	5
INTRODUCTION	7
MATERIALS AND METHODS	14
RESULTS	24
DISCUSSION	29
CONCLUSION	34
ACKNOWLEDGEMENTS	35
LITERATURE CITED	36
TABLES AND FIGURES	42
CHAPTER 3. GENERAL CONCLUSIONS	61
CONCLUSIONS	61
LITERATURE CITED	65
APPENDIX A. LIST OF ALL SPECIES FOUND WITHIN STUDY SITES.	67
APPENDIX B. VEGETATION METRICS USED IN THE NON-METRIC MULTIDIMENSIONAL SCALING ANALYSIS (NMDS) OF THE PLANT COMMUNITY.	69
APPENDIX C. MIXED LINEAR MODEL PROGRAM CODE IN SAS (SAS INSTITUTE INC. 1999) TO TEST FOR DIFFERENCES IN ENVIRONMENTAL AND VEGETATION VARIABLES BY DISTANCE FROM EDGE: (A) MODEL ACCOUNTING FOR BOTH DISTANCE FROM EDGE AND SLOPE AND (B) MODEL ACCOUNTING DISTANCE FROM EDGE ONLY.	70

APPENDIX D. R CODE FOR VECTOR FITTING ENVIRONMENTAL VARIABLES TO THE NON-METRIC MULTIDIMENSIONAL SCALING ANALYSIS (NMDS) OF THE TREE COMMUNITY.	71
APPENDIX E. R CODE FOR VECTOR FITTING ENVIRONMENTAL VARIABLES TO THE NON-METRIC MULTIDIMENSIONAL SCALING ANALYSIS (NMDS) OF THE PLANT COMMUNITY	72

## LIST OF TABLES

Table 1. Tree species importance values (IV): means and standard deviations for 17 study sites.	42
Table 2. Summary statistics from vector fitting environmental variables to the non-metric multidimensional scaling (NMDS) analysis of the tree community.	43
Table 3. Graph coordinates from vector fitting significant ( $p < 0.05$ ) environmental variables to the non-metric multidimensional scaling analysis (NMDS) of the tree community.	44
Table 4. Summary statistics from vector fitting environmental variables to the non-metric multidimensional scaling (NMDS) analysis of the plant community.	45
Table 5. Graph coordinates from vector fitting significant ( $p < 0.05$ ) environmental variables to the non-metric multidimensional scaling (NMDS) analysis of the plant community.	46
Table 6. Results of test for differences in environmental and vegetation metrics with distance from edge; slope was also included as an explanatory variable due to potential confounding.	47
Table 7. Results of test for differences in environmental and vegetation metrics with distance from edge; slope not included as an explanatory variable.	48

## LIST OF FIGURES

- Figure 1. Location of 17 study sites within the Whitewater Wildlife Management Area of southeastern Minnesota, USA. Inset: the location of Whitewater Wildlife Management Area within the Midwest Driftless Area (shaded) and the upper Midwest region. 49
- Figure 2. Axis 1 and 2 results of non-metric multidimensional scaling (NMDS) tree community analysis; environmental vectors significant to  $p=0.05$  shown. Abbreviations for vegetation and environmental variables are found in Table 3. 50
- Figure 3. Axis 1 and 2 results of non-metric multidimensional scaling (NMDS) plant community analysis; environmental vectors significant to  $p=0.05$  shown. Abbreviations for vegetation and environmental variables are found in Table 5. 51
- Figure 4. Boxplots for topographic slope by distance to forest edge. Box lengths represent an interquartile range from the 25<sup>th</sup> to the 75<sup>th</sup> percentile, the horizontal line within each box represents the median value, and the vertical lines issuing from each box extend to minimum and maximum values. 52
- Figure 5. Percent of stems within each vegetation layer (tree, sapling, shrub, and seedling) for predominant tree species: *Quercus alba* (qual), *Q. macrocarpa* (quma), *Q. rubra* (quru), *Tilia americana* (tiam), *Acer saccharum* (acsa), *Ulmus americana* (ulam), *Ostrya virginiana* (osvi), *A. negundo* (acne), and *Celtis occidentalis* (ceoc). 53
- Figure 6. Frequency and distributions of (a) *Rhamnus* and (b) *Lonicera* scores. 54

- Figure 7. Relationship between mean *Quercus macrocarpa* importance value to the mean value of *Q. alba* and *Q. rubra* combined by study site. Linear trend line also shown ( $R^2=0.46$ ). 55
- Figure 8. Relationship between mean *Rhamnus* score and mean *Quercus* importance values by study site. Linear trend lines fitted for *Q. alba* and *Q. rubra* combination ( $R^2=0.71$ ) and *Q. macrocarpa* ( $R^2=0.29$ ) shown. 56
- Figure 9. Boxplots for environmental and vegetation variables demonstrating significant ( $p \leq 0.05$ ) differences based on distance to forest edge: (a) soil magnesium, (b) soil calcium, (c) soil potassium, (d) total soil carbon, (e) total soil nitrogen, (f) *Quercus rubra* saplings, (g) *Rhamnus* score (0=absent, 1=present, 2=moderately abundant, 3=abundant, and 4=infested), (h) *R. cathartica* saplings, (i) *Acer saccharum* saplings, (j) *Ostrya virginiana* saplings, and (k) tree basal area. Examples of non significant ( $p \geq 0.05$ ) differences based on distance to forest edge are (l) *Quercus macrocarpa* importance value and (m) *Q. rubra* importance value. Box lengths represent an interquartile range from the 25<sup>th</sup> to the 75<sup>th</sup> percentile, the horizontal line within each box represents the median value, and the vertical lines issuing from each box extend to minimum and maximum values for each variable. 57
- Figure 10. Relationship between soil magnesium concentration and *Rhamnus* score (0=absent, 1=present, 2=moderately abundant, 3=abundant, and 4=infested) according to distance from edge (15, 40, 65, and 90 m). Trend lines are not significant at the  $p = 0.05$  level;  $R^2 < 0.15$  for all four distances. 60

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## CHAPTER 1.

### GENERAL INTRODUCTION

Many oak (*Quercus*) forests throughout the United States are undergoing dramatic changes as species dominance shifts from early-to-midsuccessional oak to late successional species from a variety of genera, including maple (*Acer*), beech (*Fagus*), ash (*Fraxinus*), cherry (*Prunus*), and elm (*Ulmus*) (Abrams 2003, Kessler 1992, Pallardy et al. 1988, Shotola et al. 1992, Roovers and Shifley 2003). The widespread decline of oak forests has garnered the attention of both researchers and forest managers. This concern over oak forest decline continues to grow as causal factors remain difficult to elucidate and quantify (Abrams 2003, Jacobs and Wray 2002, Lorimer 2003). Suspected causal factors include changes in fire regimes, increased consumption of acorns and herbivory of oak seedlings by burgeoning mammal populations, competition with invasive species, global climate change, forest fragmentation, and traditional oak forest management and harvest practices (Baughman and Jacobs 1992, Hansen et al. 2001, Jacobs and Wray 2002, Lopez-Barrera et al. 2006, Lorimer 2003, McNulty and Aber 2001).

A major concern surrounding the decline of oak species is the impact on both alpha and beta forest diversity. Wildlife populations are expected to decline concomitant with the loss of oak species from forest landscape, due to the loss of an important habitat and food source. These potential negative effects of oak forest decline have already been demonstrated in a comparison of avian communities in maple versus oak dominated forests. Overall avian abundance across three seasons (winter, spring, and fall) was greater in oak dominated stands. Species richness was greater in the oak stands in the spring and fall due to

foraging preferences (Rodewald and Abrams 2002), with greater insect availability in the oak stands in the spring and the mast crop available in the fall. Oaks in the central hardwood forests have been considered a keystone genus and their persistence or loss as a dominant tree species may have great consequences on the future composition of not only tree species but all the flora and fauna that directly and indirectly depend on the oak forests that have existed for the past 5000 years (Fralish 2004).

## **Oak in the Upper Midwest**

In the Upper Midwest, oak forests are an important timber resource, provide important wildlife habitat, aesthetic beauty, and protect shallow forest soils from erosion (Baughman and Jacobs 1992, Jacobs and Wray 2002). Of particular concern with oak forest decline are the population dynamics of the dominant oak species: *Quercus alba* L., *Q. macrocarpa* Michx., *Q. rubra* L. While scientists and forest professionals are currently trying to address some contributors to the decline of Upper Midwest oak forests (e.g., forest management and harvest practices, competition from other tree species, predation from animals, edge effects, and changes in fire regimes), interactions with invasive species remain largely unexplored (Baughman and Jacobs 1992, Jacobs and Wray 2002, Skally 2003). Information is particularly lacking on the role that two common exotic invasive shrubs, *R. cathartica* and *L. tartarica*, may play in oak forest decline. These shrubs are known to be highly successful invaders of Midwest habitats (Farrar 2001).

To address knowledge gaps in the causes of oak forest decline, I examined the current composition and structure of Upper Midwestern oak forests and assessed the potential effects of *R. cathartica* and *L. tartarica* on their dynamics. Due to the prominence of agricultural

fields adjacent to Midwestern oak forests, my study focuses specifically on how the invasion of these shrubs may be related to agricultural edges. Specific study objectives include: 1) ascertain the current status of oak dominance and possible oak forest decline; 2) examine the spatial dynamics of invasion by *R. cathartica* and *L. tartarica* as they relate to agricultural edges, forest structure, and forest composition; and 3) identify the potential effects of *R. cathartica* and *L. tartarica* on the present and future forest community. My goal is to provide forest managers with information on the current status of oak forest dynamics and examine the threat posed by these exotic shrub species.

## THESIS ORGANIZATION

This thesis is composed of three chapters. This first chapter is a general introduction to oak forest decline and the potential impacts of invasive shrubs in these oak forests. The second chapter contains a thorough review of oak forest and invasive shrub literature, a description of the field methods used to collect data during the summer of 2005, the statistical methods I used to analyze my data, the results of my statistical analyses, a discussion of results, and the conclusions I reached from this work. A revised version of chapter 2 will be submitted for publication in the journal *Forest Ecology and Management*. Chapter 3 contains a review of the general conclusions from my thesis research.

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CHAPTER 2.

OAK FOREST DECLINE AND EFFECTS OF TWO INVASIVE  
SHRUBS IN THE MIDWEST DRIFTLESS AREA: CURRENT  
STATUS AND IMPLICATIONS FOR THE FUTURE

A paper to be submitted to the journal *Forest Ecology and Management*

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ABSTRACT

Oak forests throughout the world are in a state of decline due to lack of oak seedling recruitment to larger size classes. Much of this recruitment decline has been attributed to changes in ecosystem disturbance regimes that have led to increased competition from other species. The Midwest Driftless Area forests in the United States are currently dominated by large oak trees of three species: *Quercus alba* L., *Q. macrocarpa* Mich., and *Q. rubra* L. These oak forests currently provide habitat for a large variety of flora and fauna, recreational opportunities for people, and an important timber resource.

We examined the current status of forest composition and structure of Midwest Driftless Area oak forests. We were specifically interested in understanding how two invasive shrubs, *Lonicera tartarica* L. and *Rhamnus cathartica* L., might contribute to the decline of oak recruitment. We found that the recruitment of oak species is poor in comparison to other canopy tree species, including *Acer saccharum* Marsh. and *Tilia americana* L., and that the majority of saplings are of non-oak species. Our results revealed

strong associations between *Q. macrocarpa*, *R. cathartica*, and sites with high levels of soil nutrients. These same site characteristics were disassociated with *Q. alba* and *Q. rubra*. *R. cathartica* was determined to have an edge effect that may place it in direct competition with oak seedlings in areas that show the most promise for oak recruitment.

Our research suggests that invasion by and competition from *R. cathartica* may be of substantial concern when managing oak stands dominated by *Q. macrocarpa*. *R. cathartica* seems to be less of a problem at present within *Q. alba*- or *Q. rubra*-dominated stands, though attention should be placed on controlling *R. cathartica* invasions from the edges of these stands.

Key words: invasive plants, *Rhamnus cathartica*, oak, oak forest decline, Midwest Driftless Area

## INTRODUCTION

Oak (*Quercus*) forests across the United States are undergoing dramatic changes as species dominance shifts from early-to-midsuccessional oak to late successional species from a variety of genera, including maple (*Acer*), beech (*Fagus*), ash (*Fraxinus*), cherry (*Prunus*), and elm (*Ulmus*) (Abrams 2003, Kessler 1992, Pallardy et al. 1988, Shotola et al. 1992, Roovers and Shifley 2003). The widespread decline of oak forests has garnered the attention of both researchers and forest managers. This concern over oak forest decline continues to grow as causal factors remain difficult to elucidate and quantify (Abrams 2003, Jacobs and Wray 2002, Lorimer 2003). Interactions between suspected causal factors of oak forest decline make the quantification of individual factors complicated. Lorimer (2003) suggests some major reasons for oak forest decline include changes in fire regimes, herbivory of oak seedlings, increased consumption of acorns by burgeoning mammal populations, and competition with invasive species. In addition, edge effects associated with forest fragmentation (Lopez-Barrera et al. 2006) and oak harvest practices, through its effects on oak regeneration, may be contributing to the decline (Baughman and Jacobs 1992, Jacobs and Wray 2002). Shaping the recent past and influencing the future of oak forests, in conjunction with all of the factors listed above, are the effects of global climate change (Hansen et al. 2001, McNulty and Aber 2001).

### **Causes of Oak Forest Decline**

Perhaps the most dramatic change affecting oak forests has been the widespread suppression of natural fire regimes. Fire suppression began in earnest around the beginning

of the twentieth century (Abrams 2003) and, because of its widespread ecological implications, has the potential to play a very large role in the decline of oak forests. Recurrent fires promoted oak forest regeneration by eliminating less fire resistant tree species, destroying seeds of competitors, and reducing overstory density (Johnson et al. 2002). However, in many areas oak recruitment is now so poor that it is unlikely that the use of prescribed fire alone will be able to restore oak as the dominant forest species (Abrams 2005). This inability of fire alone to regenerate oak forests has been demonstrated by Collins and Carson (2003) and Wendel and Smith (1986).

A variety of animal species may also have a significant role in oak forest decline. As oak populations continue to fall, acorn predators may play an increasingly large role in suppressing natural oak regeneration (Haas and Heske 2005). Invertebrate predators of acorns include acorn weevils (*Conotrachelus* spp, *Curculio* spp), nitidulids (*Stelidota* spp), acorn moths (*Valentinia* spp), and acorn gall wasps (*Cynipidae* family) (Galford et al. 1991, Johnson et al. 2002, Marquis et al. 1976). Insect predation of acorn crops can vary widely, from 10% (Steiner 1996) to as high as 100% when conditions are right (Beck 1992, Galford et al. 1991, Johnson et al. 2002), with an average consumption of around 50%. Many vertebrate species are also known to consume acorns. This predation begins even before acorns fall as birds and squirrels (*Sciurus* spp.) visiting the tree tops remove 10 – 25% of a seasons' crop (Johnson et al. 2002). Once on the ground, white-tailed deer (*Odocoileus virginianus*), mice (*Peromyscus* spp.), chipmunks (*Tamias* spp.), squirrels, raccoons (*Procyon lotor*), and over 30 bird species, principally blue jays (*Cyanocitta cristata*), wild turkeys (*Meleagris gallopavo*) and wood ducks (*Aix sponsa*), are most often cited as dominant acorn consumers (Haas and Heske 2005, Johnson et al. 2002, McShea 2000). Only

in years of high acorn production are oak trees able to achieve reproductive success by overwhelming acorn predators (Johnson et al. 2002). However, for acorns that survive long enough to germinate, white-tailed deer herbivory contributes to high seedling mortality rates (Collins and Carson 2003, Marquis et al. 1976, Russell and Fowler 2004).

Invasive species are having increasing impacts on our native oak woodlands and are one of the leading causes of species endangerment in the United States (Czech and Krausman 1997). Although interactions with herbaceous plant species may not play a significant role in oak decline (Lorimer et al. 1994), woody species (both native and non-native) have been shown to negatively affect native tree seedling establishment (Lorimer et al. 1994, Woods 1993). In addition to direct competition, invasive plant species are known to alter forest fire regimes, leaf litter accumulation, nutrient cycling, hydrology, microbial community composition, and overall energy budgets (Heneghan et al. 2004, Mack et al. 2000).

Forest fragmentation and subsequent edge effects may contribute to oak forest decline, especially in areas where forestland is undergoing high rates of parcelization and development, which is true of most privately-owned forestlands in the U.S. (Hansen et al. 2005, Mehmood and Zhang 2001). Edge effects include a suite of interrelated factors that vary according to edge orientation and the degree of contrast between the forestland and its surrounding land cover (known as “edge contrast”) (Cadenasso et al. 2003). Edge orientation principally determines the strength of the edge effect. In northern latitudes, the contrast between north-facing edges and south-facing edges can be great due to greater differences in solar energy availability. These effects are weaker closer to the equator due to the higher angle of the sun relative to the landscape (Foreman 1995, Ries et al. 2004). Edge contrast can have a strong influence on the overall effect an edge has on surrounding environments.

The influence of an edge is generally greater with “hard” (high-contrast) edges when compared to “soft” (low-contrast) edges (Strayer et al. 2003). These differences are attributed to variation in surrounding vegetation height and vegetation densities within the same edge type (Foreman 1995, Ries et al. 2004). Together, edge orientation and contrast lead to differences in microclimate, specifically solar radiation and wind, which in turn strongly influence vegetation composition (Muria 1995, Palik and Murphy 1990, Ries et al. 2004). Both solar radiation and wind desiccate leaves and increase evapotranspiration rates, affecting plant species survival and growth within edges. The availability of sunlight also affects vegetation composition, based on species competitive ability and shade tolerance (Muria 1995, Honnay et al. 2002, McDonald and Urban 2006). Together, edge orientation, edge contrast, and microclimate, work to determine the depth of influence an edge will have on a forest. The impact of an edge can also vary widely depending on species under consideration (Brothers and Spingarn 1992, Debinski and Holt 2000, Ries et al. 2004). For example, Reis et al. (2004) reviewed abiotic and vegetation responses to edge up to 50 m into forest patches, while bird response extended up to 200 m. Depth of edge influence is an important consideration in highly fragmented forests as small patches may contain little “core” area and function essentially as all edge, offering little in terms of conservation value (Brothers and Spingarn 1992, Debinski and Holt 2000, Lindenmayer and Franklin 2002). One important consideration with edge effects is that the entire suite of impacts associated with fragmentation may remain veiled unless long term studies are completed (Debinski and Holt 2000).

Forest fragmentation and edge effects have important implications for oak forest management because of associated differences in the survivability of oak seedlings and the

higher potential for the establishment of invasive plant species. “Soft” (low-contrast) edges have been shown to produce vigorous oak seedling development in comparison to abrupt, or “hard,” edges; however, “hard” edges have been shown to have higher oak seedling survival (López-Barrera et al. 2006). Numerous studies document higher occurrences of invasive species at forest edges (Flory and Clay 2006, Hester and Hobbs 1995, Honu and Gibson 2006, Moffat 2004). Regardless of edge contrast, invasive plant diversity and occurrence is greater in both quantity and distance infiltrated from edge on warmer, south-facing edges than cooler, north-facing edges (Brothers and Spingarn 1992, Honnay et al. 2002). Several studies have demonstrated patterns of forest invasion by exotic plants from agricultural and road edges (Brothers and Spingarn 1992, Flory and Clay 2006, Honnay et al. 2002). The impact of the establishment of these exotic plants on oak seedling survival is largely unknown.

Improper forest management is a contributing factor to oak forest decline. High-grading, a practice of removing only those trees of highest market value and leaving the remaining timber standing leaves poor quality trees that have little potential for future merchantable timber and ignores requirements for oak regeneration (Jacobs and Wray 2002). A growing body of work is demonstrating that with proper management (e.g., understory thinning, prescribed fire, selective harvest), some degree of oak regeneration can be attained (Fralish 2004, Lorimer et al. 1994, Stan 2006). Yeagle and Groninger (2006) have shown that, without proper management, oak dominance of a forest site can be lost in a single cutover. Competition with other woody species is a strong causal factor in the decline of oak dominance (Abrams 2003, Lorimer et al. 1994, Pallardy et al. 1988, Shotola et al. 1992); thus, management of woody species in the forest understory is of primary importance in

facilitating oak forest regeneration (Fralish 2004, Lorimer et al. 1994, Stan 2006). When comparing oak forest stands without shade tolerant understory saplings to stands with shade tolerant understory saplings there is a 90% decrease in species richness and cover (Fralish 2004).

Global climate change models have indicated large potential redistributions of tree species as average annual temperatures are predicted to increase 3.3 – 5.8°C with increases in atmospheric CO<sub>2</sub> (Hansen et al. 2001, He et al. 2002, Iverson and Prasad 1998). Changes in average annual temperatures alter carbon, water, and nutrient cycles and will result in the redistribution of tree species ranges over time. This is an area of ongoing investigation, as it is expected the predictive power of global climate change models is limited at present (Hansen et al. 2001, He et al. 2002, Iverson et al. 2004). Although dramatic shifts in tree species is a common prediction, an assemblage of factors might inhibit these shifts, including the long reproductive life cycles of trees compared to the short-lived species that have already shown genetic shifts in response to climate change (Bradshaw and Holzapfel 2006), range expansion of destructive forest pathogens (Bergot et al. 2004), and loss of animal species needed for tree species dispersal (Iverson et al. 2004). As the effects of anthropogenically-induced global climate change become more pronounced, interactions between climate and land use will likely play key roles in determining which species will adapt *in situ*, redistribute, or decline (Hansen et al. 2001).

## **Oak in the Upper Midwest**

In the Upper Midwest, oak forest decline is a major concern of natural resource managers as these forests provide an important timber resource, wildlife habitat and food

source, aesthetic beauty, and protect shallow forest soils from erosion (Baughman and Jacobs 1992, Jacobs and Wray 2002). Of particular concern are the downward population trends of the dominant oak species *Quercus alba* L., *Q. macrocarpa* Michx., *Q. rubra* L. (Jacobs and Wray 1992). While scientists and forest professionals are addressing some contributors to the decline of these species (e.g., forest management and harvest practices, competition from other tree species, predation from animals, edge effects, and changes in fire regimes), interactions with invasive species remain largely unexplored (Baughman and Jacobs 1992, Jacobs and Wray 2002, Skally 2003). Information is particularly lacking on the role that two common exotic invasive shrubs, *R. cathartica* and *L. tartarica*, may play in the decline. *R. cathartica* and *L. tartarica* are commonly found throughout the Upper Midwest and are known to be good invaders of Midwest habitats (Farrar 2001). Such invasive exotic species are expected to have both large negative economic and ecological impacts, even if not always quantified (Pimentel et al. 2000), and, along with development and agriculture, the exotic invasive species are considered one of the top reasons for species endangerment in the United States (Czech and Krausman 1997). Invasive species have been shown to decrease native species density and have an overall negative effect on community diversity (Meiners et al. 2002, Rooney et al. 2004). Currently, there is no empirical evidence of *R. cathartica* or *L. tartarica* facilitating establishment of any native species.

To address gaps in our understanding of Upper Midwestern oak forest decline and impacts of invasive species we examined the current composition and structure of oak forests in southeastern Minnesota and assessed the effects of *R. cathartica* and *L. tartarica* on oak forest dynamics. Due to the prominence of agricultural fields adjacent to remaining oak forests in the Midwest, our study focused specifically on how the effects of these invasive

shrubs may be related to agricultural edges. Agricultural edges are expected to be key source areas of these invasive shrubs. Specific study objectives included to: 1) ascertain the current status of oak dominance and possible oak forest decline; 2) examine the spatial dynamics of invasion by *R. cathartica* and *L. tartarica* as they relate to agricultural edges, forest structure, and forest composition; and 3) identify the potential effects of *R. cathartica* and *L. tartarica* on present and future forest community composition. Our overall goal was to inform managers of oak forest systems about the threat posed by these exotic shrub species. Our sampling methodology specifically addressed some of the common edge and fragmentation study shortcomings outlined in Muria (1995). These included selecting appropriate replicates based on forest age, stand size, and composition, avoiding topographic accidents (e.g. streams, large depressions) and careful delineation of transect start points based on the location of canopy tree trunks.

## MATERIALS AND METHODS

### **Study Area**

This study was completed in the Whitewater Wildlife Management Area (WMA) of Minnesota, USA (Figure 1), which lies within the Midwest Driftless Area. The Driftless Area is a unique landform in the region that encompasses over 4 million hectares of land in SE Minnesota, SW Wisconsin, NE Iowa, and NW Illinois, and has a high proportion of forest cover in comparison to surrounding regions (Vogelmann et al. 2001). Although colloquially referred to as the Driftless Area, evidence of pre-Illinoian glacial drift over 500,000 years old has been identified in parts of the area (Albert 1995, Hobbs 1999). Our study area falls along

the border of what is hypothesized to be a truly driftless area and what is referred to as the pseudo-driftless area, which has evidence of some pre-Illinoian glaciation (Hobbs 1999). This area is typified by deep valleys with steep hillsides and flat topped bluffs. Much of the lowlands and bluff tops have been cleared for agriculture, but the steep hillsides remain in forest that comprises approximately 1.3 million hectares (33 %) of the region (Jacobs and Wray 1992).

The 10,900-hectare Whitewater WMA is located 40 kilometers east of Rochester, MN, in Winona, Wabasha, and Olmsted counties. Although the focus of WMA activity is providing food and cover for wildlife, it also generates goods and services for direct human consumption. The area is open to commercial timber and fuelwood harvesting, and some areas of the WMA are also leased to farmers for agricultural production of corn, soybeans, and hay. Whitewater WMA is also open to recreational activities including hunting, fishing, bird-watching, picking fruits and mushrooms, and cross-country skiing.

Whitewater WMA and surrounding areas experience a continental climate with annual average precipitation of 80 cm; growing seasons range from 130 to 170 days (Albert 1995). Approximately 90 percent of the surrounding landscape is now used for row crop agriculture or pasture. Ten percent of this landscape is in floodplain, maple-basswood, oak, and white-pine forest. Many of these forests have been grazed to various degrees during the past century. Occasional remnants of bluff prairie, dry oak savanna and dry prairie can still be found throughout the Driftless Area. Major soil classifications include Udalfs on ridge tops and Orthents on flood plains (Albert 1995). Loess thickness can vary from less than 30 cm on valley walls to up to 6 m on ridge tops. Unique and dramatic exposures of Ordovician dolomite, limestone, and sandstone bedrock are common in steep ravines (Albert 1995).

## Field Methods

Within Whitewater WMA, we selected 17 dry to mesic oak forest stands representing a wide range in aspects for sampling. All selected stands were designated as oak forest by the Minnesota Department of Natural Resources (DNR) forest inventory cooperative stand assessment and were located adjacent to an agricultural edge. Agricultural edges were defined as the boundary between a forest stand and either a crop field (e.g., corn, soybean, alfalfa, hay) or a filter strip adjacent to a crop field. In order to minimize effects from any adjacent edges, forest stands were selected only if they were at least 250 m wide and 200 m deep. Oak forests with white pine (*Pinus strobus*) and red pine (*Pinus resinosa*) plantings adjacent to crop edges were avoided. All sampling was conducted after canopy closure, from mid-June through August 2005.

We established our stand-level sampling framework at the approximate midpoint of the stand along the agricultural edge, based on stand assessment maps. Our sampling framework consisted of three transects perpendicular to the edge with four sampling plots on each transect, located 15 m, 40 m, 65 m, and 90 m from the agricultural edge. The midpoint of the stand edge corresponded to the start point of the middle transect; the other two transects were located 25 meters to each side of the middle transect. Transect start points were located where the first three to five trees diameter at breast height (dbh, 1.5m from ground level)  $\geq 10$  cm were encountered when moving from the agricultural land into the forest stand. From each of the three transect start points, we used a compass and meter tape

to layout transects into the forest stand along a bearing perpendicular to the forest edge; this bearing is henceforth referred to as the agricultural edge aspect.

At each of the four sampling plot distances, we established 200 m<sup>2</sup> circular tree plots and recorded species and dbh of all trees  $\geq 10$  cm dbh. If trees were at the edge of the plot, we recorded trees whose centers at breast height were at or inside the 7.98 m sampling radius. We identified and counted saplings, defined as having a dbh  $\geq 2.5$  cm and  $< 10$  cm, in a 150 m<sup>2</sup> circular plot (6.91 m sampling radius) concentric within the tree plot.

We sampled shrubs, defined as woody species less than 2.5 cm dbh and at least 0.5-m tall, in two 5-m<sup>2</sup> circular plots at each of the four distances from the forest edge. Centers for these 5-m<sup>2</sup> circular plots were located 5-m from each sampling plot center and approximately perpendicular to the transect. We recorded stem counts and species of all defined shrubs with the exception of dogwood (*Cornus* spp.) and gooseberry (*Ribes* spp.) species, which were recorded to genus.

We made a visual assessment of invasive shrub density using invasive shrub ratings for *Rhamnus cathartica* and *Lonicera tartarica* in each 200-m<sup>2</sup> tree plot. Ratings used for each species ranged from 0 to 4, with 0=absent, 1=present, 2=moderately abundant, 3=abundant, and 4=infested. As an approximation of age and time since invasion, we recorded the basal diameter of the largest *R. cathartica* in each 200 m<sup>2</sup> tree plot.

We estimated total cover for vegetation less than 0.5-m tall at four 1.0-m<sup>2</sup> vegetation quadrats. A 1.0-m by 1.0-m sampling frame was constructed with legs that elevated the frame 0.5 meter above the ground. Placement for the vegetation quadrat frame was determined by measuring three meters NE, SE, SW, and NW from each sampling plot center. The quadrat frame was placed consistently in the same position relative to the direction from

the plot center (NE, SE, SW, or NW). Within this quadrat, percent cover was estimated for the following categories:

- Herbaceous cover—all herbaceous plant cover including that >0.5 m tall;
- Live woody cover—tree stems and woody shrub cover <0.5 m tall;
- Tree seedling cover—canopy tree seedling cover for all tree species <0.5 m tall;
- Coarse woody debris (CWD)—dead wood including stems, branches or sheets of bark; and
- Rock cover—area represented by exposed rock surfaces.

Within the vegetation quadrat, species and stem counts were recorded for all canopy tree seedlings. In order to maintain consistency, all vegetation cover estimates were conducted by one individual (E.C.M.).

We collected four short core soil samples (11.5 cm deep and 5.9 cm in diameter) in each of the cardinal directions (N, S, E, and W) 3 m from the tree plot center; the four subsamples were combined into one composite sample to eliminate fine scale variability. Samples were double bagged and placed in a 4°C cold room within one week of sampling. We measured soil sample bulk density by drying the soil samples at 40°C overnight and recording the weight of the samples to the nearest 0.1 g. Soil samples were then analyzed at the Iowa State University Soil and Plant Analysis Laboratory for total carbon, total nitrogen, pH and sodium, calcium, magnesium, and potassium concentrations.

We recorded slope to the nearest degree at each tree plot center using a Suunto height and slope angle meter model PM-5/66 P. Slope measurements were taken at each tree plot center covering the 20.12 meters (66 feet) towards (exterior slope) and away from (interior slope) the agricultural edge. We estimated canopy cover at each tree plot center using a

convex spherical densitometer. Canopy cover was estimated four times, once in each of the four cardinal directions (N, S, E, and W), and then averaged. To minimize error, canopy cover was always estimated by the same individual (E.C.M.) throughout the season.

At each plot, the following observations were noted as they might provide insight into differing anthropogenic and natural histories at each site. Within and around each tree plot, we recorded qualitative observations on the presence of old hillside roads, locations of barbed wire, presence of oak trees with oak wilt symptoms and canopy tree blowdowns. The entire stand was also walked and sketched; qualitative observations on general forest composition, dominant vegetation types, overall invasive shrub dominance, locations of barbed wire, old hillside road locations and any indications that the current agricultural edge was not the same as the historic agricultural edge (indicated by notably younger trees at the edge, old plow lines, terraced slope, etc.) were recorded.

Where topography and tree cover allowed, we recorded global positioning system (GPS) locations of each marking flag in Universal Transverse Mercator units with a TRIMBLE GeoXT for potential relocation.

## **Data Analysis**

### ***Oak forest composition, structure and community relationships***

We calculated importance values (Table 1) for trees  $\geq 10$  cm dbh to compare the overstory communities among our sampling sites. Importance value is considered a holistic measure of overstory community conditions, as it combines both compositional and structural information (Curtis 1971). We used a combination of relative dominance and relative density in calculating importance value according to the following formula:

$$\text{Importance Value} = \left[ \left( \frac{\text{Basal area total for a tree species}}{\text{Total basal area of all trees}} \right) + \left( \frac{\text{Number of trees of a species}}{\text{Total number of all trees}} \right) \right] / 2.$$

These calculated importance values allowed for a single composite measure to be used in our statistical analyses.

Solar radiation plays a key role in determining strength and depth of edge effects (Ries et al. 2004). To account for variation in solar radiation by edge aspect we calculated the Heat Load Index (HLI) (Jeffries et al. 2006, McCune and Keon 2002) for each sampled stand. Heat load index was calculated for each agricultural edge aspect using the formula:

$$\text{Heat load index} = (1 - \cos[\theta - 45]) / 2.$$

This equation uses the site agricultural edge aspect as  $\theta$  and transforms it to a number between zero and one, with zero corresponding to the coolest northeast facing slopes and one corresponding to the warmest southeast facing slope.

We employed non-metric multidimensional scaling (NMDS) to examine compositional differences among sites, tree species, invasive shrub scores, and environmental variables. We chose NMDS as an analytical tool as it avoids assumptions of linear relationships, uses ranked distances among data, and allows for the use of the distance measure best suited to specific ecological community data (McCune and Grace 2002). Our NMDS analyses were performed using the Vegan package in the statistical program R version 2.3.1 (R Development Core Team 2006). We used Bray-Curtis distance as a distance

measure in our NMDS analysis because it is generally regarded as a robust measure for ecological community data (McCune and Grace 2002). We ran two NMDS analyses: one using all tree importance values calculated for each site (hereafter called ‘Tree NMDS’) and a second using a combination of vegetation data (see next paragraph for tree, sapling, and shrub data utilized; hereafter called ‘Vegetation NMDS’). The final stress of the Tree NMDS was 11.6, which is reasonable for ecological community data (McCune and Grace 2002). We added environmental data (i.e., canopy cover, total tree basal area, herbaceous cover percents, slope, heat load index, total soil carbon, total soil nitrogen, soil pH, soil bulk density, and soil sodium, calcium, magnesium, and potassium concentrations) and qualitative measures of invasive species (*Rhamnus* score and *Lonicera* score) as regressed vector arrows (Figure 2). The length of each arrow is proportional to the correlation between the variable and the ordination; the direction of the arrow indicates the gradient of change for the variable. We display vectors that are significantly correlated with the ordination at  $p \leq 0.05$  after 1000 permutations (p-values for all vectors are shown in Table 2; species and vector NMDS coordinates shown in Table 3).

We selected dominant tree, sapling, and shrub data for the Combined Vegetation NMDS analysis based on the following criteria:

1. Tree species that represented  $\geq 5\%$  of the total importance values across all sites were included. This cutoff allowed the inclusion of all three dominant oak species of interest. This cutoff also eliminated infrequently sampled species of lower significance. Five tree species met this criterion and together represent 72.9% of total tree importance, including *Q. rubra*, *U. americana*, *Q. macrocarpa*, *T. americana*, and *Q. alba*.

2. Sapling species that represented  $\geq 5\%$  of the total sapling stems across all sites were included. Eight sapling species met this criterion and together represented 97.1% of the total saplings, including *U. Americana*, *T. Americana*, *Ostrya virginiana*, *R. cathartica*, *Prunus serotina*, *Acer negundo*, *Acer negundo*, *Celtis occidentalis*, and *A. saccharum*.
3. Shrub species that represented  $\geq 5\%$  of the total shrub stems counted across all sites were included. Six shrub species met this criterion and together represented 76.9% of all shrub stems, including *Ribes* spp., *R. cathartica*, *Cornus* spp., *P. virginiana*, *U. americana*, and *Zanthoxylum americanum*.

The 5% cutoff was chosen based on natural breaks in the data and because it met our objective of incorporating dominant species. This NMDS analysis was performed to develop a holistic understanding of the interactions among tree, sapling, and shrub vegetation layers and the environment within our data. The Combined Vegetation NMDS (Figure 3) was also run using the Vegan package in the statistical program R version 2.3.1 (R Development Core Team 2006). The final stress of this NMDS was 10.4. As in the Tree NMDS, environmental data and measures of invasive species were added as regressed vector arrows. Vectors displayed had a significance of  $p \leq 0.05$  after 1000 permutations (p-values for all vectors are shown in Table 4; species and vector NMDS coordinates shown in Table 5).

### ***Spatial Distribution of Vegetation and Environmental metrics***

To determine the effects of edge, we included the following variables in first-order autoregressions in SAS (SAS Institute Inc. 1999): (1) the three dominant *Quercus* species (*Q. alba*, *Q. macrocarpa*, and *Q. rubra*), (2) measures of the invasive shrubs *R. cathartica* and *L.*

*tartarica*, (3) environmental metrics, and (4) *O. virginiana* and *A. saccharum* sapling densities. Variables were included in this analysis based on our original study goals and key results from the NMDS analysis. Because of the topographic and land use contexts in which our study sites lay, with bluff tops in agricultural cover and forests on hillsides that tend to steepen down slope, the factor of distance from edge tends to be highly correlated with slope (Figure 4). In the case of some ecological processes, this high correlation may result in the confounding of factors (i.e., nutrient levels may vary with either distance from edge or slope; (Birkeland 1984, Chen et al. 1997), and in other cases not (i.e., we expect *R. cathartica* to respond more to edge, because of light and disturbance dynamics, and not to slope, because it is bird dispersed (Archibold et al. 1997, Czarapata 2005). Hence, we developed two statistical models to separate these effects, one including both distance from edge and slope (Table 6; Appendix C) and the other containing only distance from edge (Table 7; Appendix C). This approach allowed us to account for slope in cases where slope may be confounded with distance from edge and then allowed us to examine cases where edge effects were thought to be the primary driver of observed results. The specific nature of these statistical models cannot conclusively answer the question of whether slope or distance from edge is the primary driver for a specific result. We use biological insight derived from other research to decide whether or not slope, distance from edge, or some other untested driver is the most likely reason for observed results. We excluded one of our seventeen sites from this analysis since it was the only site with an agricultural edge at the bottom of a slope; the agricultural edge was at the top of the slope for the remaining 16 sites.

The first-order autoregression procedure we used accounts for autocorrelation within the data by assuming that measures spatially closer to one another are more highly correlated

than measures further apart. Thus, this analysis allowed us to account for autocorrelation due to spatial proximity of our sampling points and demonstrate differences due to edge effects.

We used the MIXED linear model (SAS Institute Inc. 1999) with our most interior forest plot (Plot 4, located 90 m from the agricultural edge) as our baseline; measurements from each of the other three plots (15 m, 40 m and 65 m) are statistically compared to this baseline.

Within our model, both distance from edge and slope (when included) served as explanatory variables in our test for differences among a select subset of vegetation and environmental variables (*Q. alba*, *Q. macrocarpa*, and *Q. rubra* trees and saplings; *O. virginiana* and *A. saccharum* saplings; measures of the invasive shrubs *R. cathartica* and *L. tartarica*; environmental metrics).

## RESULTS

### **Oak forest composition and structure**

We recorded a total of 27 trees species across the 17 oak forest stands we sampled. Of these 27 species, only *Q. alba*, *Q. macrocarpa*, *Q. rubra*, *T. americana*, and *U. americana* had average importance values of  $\geq 5\%$ . Fourteen of the 27 species were relatively uncommon with average importance values below 1.0 (Table 1). Twenty-five of 27 species have standard deviations greater than or equal to their importance value demonstrating high intersite variability (Table 1). Two exceptions were *Q. rubra* and *U. americana*, which were found frequently throughout the 17 sites.

Relative percent tree, sapling, shrub, and seedling stem counts per hectare for nine selected canopy species show a forest converting from dominance by oak to dominance by

more mesic, shade tolerant species, including *Acer saccharum*, *T. americana*, *U. americana*, and *A. negundo* (Figure 5). Oak species, including *Q. alba*, *Q. macrocarpa*, and *Q. rubra*, were the most abundant in the tree size class within our stands, and represented 96%, 80%, and 75% of each species stem counts, respectively. *A. saccharum*, *T. americana*, and *O. virginiana*, were most abundant in the sapling size class, representing 57%, 52%, and 47% of all stem counts, respectively. *C. occidentalis*, *U. americana*, and *A. negundo* were relatively most abundant as seedlings, represented by 55%, 49%, and 37% of all stem counts, respectively.

*Q. rubra* was present at all sites and had the highest average importance value at 31% (Table 1). *U. americana* (16%) and *Q. macrocarpa* (14%) had the next two highest averages and were each present at 16 of 17 sites. Sapling stem counts were dominated by *U. americana*, which represented 28% of all saplings, followed by *T. americana* (16%) and *O. virginiana* (13%). Species from the genus *Ribes* represented 43% of shrub stems, followed by *R. cathartica* at 11%.

## **Invasive Shrubs**

*R. cathartica* was found as a frequent contributor to both the sapling and shrubs size categories. As a sapling *R. cathartica* represented 10.3% of all sapling stems measured with as few as zero stems to as many as 256 stems/ha recorded at different sites (mean = 44 stems/ha; standard deviation = 73 stems/ha). As a shrub, *R. cathartica* represented the second most frequently recorded species with 11% of all shrub stems (mean = 1,650 shrubs/ha; standard deviation = 3,800 shrubs/ha). Fifty percent of the 200 m<sup>2</sup> tree plots contained a sample of *R. cathartica* with an average diameter of 4.5 cm with a standard

deviation of 3.0 cm. *L. tartarica* was sampled as a shrub at five of 17 sites and a mere total of 15 individual shrubs in this study. The mean density of *L. tartarica* was 74 shrubs/ha (standard deviation = 169 shrubs/ha). *Rhamnus* score (0=absent, 1=present, 2=moderately abundant, 3=abundant, and 4=infested) had a median of one with a mode of zero while *Lonicera* score had a median and mode both of zero. Frequency distributions of *Rhamnus* and *Lonicera* scores demonstrated trends of both species being less abundant with increasing distance from edge (Figure 6 a, b).

### Community relationships

The Tree NMDS reveals a positive association between *Q. alba* and *Q. rubra*; both are concomitantly negatively associated with *Q. macrocarpa* (Figure 2). Both *Q. alba* and *Q. rubra* are also positively associated with *O. virginiana* and *A. saccharum*. The several species appearing near the edges of the Tree NMDS were present in low numbers at only one site (e.g. *Crataegus* spp., *Juniperus virginiana* L., *Prunus pensylvanica*, *Quercus palustris*), although lack of commonness did not assure a species would be found away from the center of the Tree NMDS (e.g., *Fraxinus nigra* and *Robinia pseudoacacia*; Figure 2). The *Rhamnus* score (rs) vector was strongly negatively associated with tree basal area (tb). The *Lonicera* score vector was not significant ( $p \leq 0.05$ ). With the exception of sodium, soil nutrients and soil pH were positively associated with one another (tc, tn, c, pH, k, m) (Figure 2).

The Vegetation NMDS (Figure 3) reveals salient trends in forest composition across our study sites. Of primary importance, our qualitative measure of *R. cathartica* infestation (rs) had a vector significance of  $p < 0.01$  (Table 4) and appears between two quantitative measures of *R. cathartica*; *R. cathartica* sapling (rhcap) and shrub (rhcash) densities.

*Rhamnus* score is strongly associated with greater importance of *Q. macrocarpa* and statistically significant vectors ( $p \leq 0.05$ ) for higher soil pH, total nitrogen, and calcium concentration. *Rhamnus* score was also associated with other soil nutrients not significant at the  $p \leq 0.05$  (total carbon, potassium concentration, and magnesium concentration; Table 4). Higher levels of *R. cathartica* were disassociated with sites dominated by *Q. alba* and *Q. rubra* trees, *O. virginiana* saplings, or sites with high total tree basal area (tb).

As demonstrated above, dominance by *Q. alba*, *Q. rubra* or a combination of the two species was a good indicator that *Q. macrocarpa* and *R. cathartica* would not be found as an important contributor to forest composition at a given site. This disassociation is demonstrated graphically (Figure 7). As combined *Q. alba* and *Q. rubra* average site importance values increase, *Q. macrocarpa* average site importance values decrease. A linear trend line fit these data ( $r^2=0.46$ ). *Rhamnus* score decreases concomitantly with increases in the combined importance values of *Q. alba* and *Q. rubra* (Figure 8). A linear trend line fit to these data has an  $r^2=0.71$ . Although not as strong (linear trend line  $r^2=0.29$ ), *Q. macrocarpa* importance values increase with *Rhamnus* score.

### **Spatial Distribution of Vegetation and Environmental metrics**

Four of 21 vegetation and environmental metrics demonstrated statistical significance for distance from edge ( $p \leq 0.05$ ) and six metrics demonstrated statistical significance ( $p \leq 0.05$ ) with slope (Table 6). Of the four metrics that showed a response to edge, two were measures of vegetation (tree basal area, *Q. rubra* sapling stem count) while the other two metrics were environmental (soil magnesium concentration, total soil carbon). All six metrics that were significantly associated with slope were measures of soil characteristics

(magnesium, calcium, and potassium concentrations, pH, total carbon, and total nitrogen). No vegetation metrics showed significant differences by slope alone (Table 6), suggesting that distance from edge and slope are not confounded for these measures.

Using only distance from edge as an explanatory variable, significant edge effects were found for 12 of 22 metrics tested (Table 7). Significant ( $p < 0.01$ ) differences were seen in the environmental variables of slope (Figure 4), soil magnesium, calcium, and potassium concentrations, total soil carbon, and total soil nitrogen (Figure 9 a-e). Soil nutrients increased with distance from edge, with all but sodium demonstrating significant differences from edge; however, as the results of the above model show, many of these differences are due to slope rather than distance from edge (Table 6).

*Q. rubra* saplings, *Rhamnus* score, and *R. cathartica* saplings demonstrated a response to distance from edge ( $p < 0.01$  for *Q. rubra* and *Rhamnus* score;  $p < 0.05$  for *R. cathartica*) with only the 15 m plot differing significantly from the interior forest plot ( $p < 0.01$  for *Q. rubra*;  $p < 0.05$  for *R. cathartica*) (Table 7, Figure 8f-h). Most *Q. rubra* saplings were found in the 15 m plots (Figure 8f). *A. saccharum* and *O. virginiana* saplings demonstrated a response to edge ( $p < 0.01$  for *A. saccharum*;  $p < 0.05$  for *O. virginiana*). *A. saccharum* had significantly lower numbers of saplings in the 15 m ( $p < 0.01$ ) and 40 m ( $p < 0.05$ ) plots when compared to the 90 m plot (Table 7, Figure 8i) while *O. virginiana* had significantly ( $p < 0.01$ ) lower numbers of saplings in the 15 m when compared to the 90 m plot (Table 7, Figure 8j). Tree basal area demonstrated a response to edge ( $p < 0.01$ ) with the 15 m and 40 m plots having significantly ( $p < 0.01$ ) higher tree basal areas when compared to the 90 m plot (Table 7, Figure 8k). *Lonicera* score and importance values for *Q. alba*, *Q.*

*macrocarpa* (Figure 8l), and *Q. rubra* (Figure 8m) did not differ significantly ( $p > 0.05$ ) based on distance from edge (Table 7).

## DISCUSSION

### **Oak forest composition and structure**

Our study supports trends observed in other forests experiencing oak forest decline (Pallardy et al. 1988, Roovers and Shifley 2003, Stan et al. 2006, Shotola et al. 1992), in which smaller size classes are dominated by non-oak species (Figure 5). While oak species comprise the majority of the importance on these sites (Table 1), these stands are dominated by large individuals of *Q. alba*, *Q. rubra*, and *Q. macrocarpa*, which are relatively few in number. Few individuals of these species are found within the sapling and seedling layers (Figure 5). Concurrently, shade tolerant species (e.g., *A. saccharum*, *T. americana*, *U. americana*) are experiencing good recruitment to sapling and seedling size classes, which may result in dominance by these species in the future. *U. americana* already comprises 16.3% of the site importance. Although the number of oak seedlings we recorded was similar in number to seedlings of *A. saccharum* and *T. americana*, the oak seedlings do comparatively not appear to be recruiting to sapling size (Figure 5). Seedling numbers are dominated by *U. americana* and *C. occidentalis* at present (Figure 5), suggesting another potential shift in composition in the future. Increases in *U. americana* and *C. occidentalis* have been documented in conjunction with the decline of oak species as canopy dominants (Pierce et al. 2006).

The two invasive shrubs *R. cathartica* and *L. tartarica* we studied differed greatly in their abundance and potential impacts within our studied oak forest. We found *L. tartarica* within only five of the 17 stands sampled, and then only at low densities and were most predominantly located at the forest edge (Figure 6b); thus, *L. tartarica* did not appear to play a significant role in our oak forest stands at present. Anecdotally, *L. tartarica* dominated areas of very high light including extreme outer edges and shrub dominated areas lacking significant tree cover, habitats not covered by this study. Although much more prevalent (representing over 10% of both saplings and shrub stems), we did not find *R. cathartica* distributed evenly among the oak forest stands. *R. cathartica* was strongly associated with *Q. macrocarpa* importance and higher site nutrient levels while strong presence of *Q. alba* and *Q. rubra* was strongly associated with low levels of *R. cathartica*. This finding may facilitate a focused approach to minimizing the impacts and spread of this invasive shrub. The strong association of *R. cathartica* with *Q. macrocarpa* may allow managers to use forest inventory cooperative stand assessment data to identify areas that may be experiencing significant levels of *R. cathartica* invasion.

## **Community relationships**

### ***Oak forest composition, structure and community relationships***

We observed significant associations between *Q. alba*, *Q. rubra* and *O. virginiana* (Figure 2 and 3). The association of *O. virginiana* with *Q. alba* and *Q. rubra* is not unusual as *O. virginiana* is a common understory tree within oak forests (Barnes and Warren 1981). *Q. macrocarpa* and *R. cathartica* were significantly associated with each other. Importantly, the *Q. macrocarpa* and *R. cathartica* association was negatively associated with *Q. alba*, *Q.*

*rubra* and *O. virginiana* association (Figure 2 and 3). *Q. macrocarpa* is one of the most drought tolerant oak species in the United States and this may account for its presence at sites not having large components of either *Q. alba* or *Q. rubra*, which are not as drought tolerant (Stein et al. 2003). The strong association of *Q. macrocarpa* with *R. cathartica* included sites having (generally) higher soil nutrient levels. This association with soil nutrients has been observed with many other invasive plant species (Howard et al. 2004).

### ***Spatial Distribution of Vegetation and Environmental metrics***

When edge effects and slope are taken together, six of seven soil metrics show significance ( $p < 0.05$ ) with slope while only two of these soil metrics show significance ( $p < 0.05$ ) with edge (Table 6). However, when only edge effects are considered, five of these seven soil metrics show a significant ( $p < 0.05$ ) correlation with edge (Table 7). In the case of our soil metrics, the model accounting for the slope effect is more appropriate—soil metrics have been shown to increase down slope due to leaching and/or erosional processes (Birkeland 1984, Chen 1997). Yet, percent total carbon and magnesium concentration significantly increase with distance from edge even when the slope effect is accounted for.

Oak importance values for *Q. alba*, *Q. rubra*, and *Q. macrocarpa* along with *Q. alba* and *Q. macrocarpa* saplings did not demonstrate a significant difference with either slope or edge effects (Tables 6 and 7; Figure 8l, m). These results indicate that within our oak forests that oak tree species were distributed relatively evenly throughout the forest. However, *Q. rubra* saplings did demonstrate a significant edge effect (Tables 6 and 7), likely due to higher light availability near the high contrast edges of these forests. *Q. rubra*, like most oaks, is considered relatively intolerant of shade (Johnson et al. 2002). In our most exterior (15 m)

plot, we recorded slightly lower mean canopy cover (84%) and higher variation (standard deviation = 6.2%) when compared to interior plots (canopy cover: 40 m mean = 86%, standard deviation = 5.5; 65 m mean = 87%, standard deviation = 5.3; 90 m mean = 86%; standard deviation = 5.7%). This variability combined with additional light filtering in from the edge might allow the *Q. rubra* saplings adequate light, whereas in the more interior plots there is apparently not enough light for *Q. rubra* seedlings to survive to sapling size. One likely reason *Q. alba* and *Q. macrocarpa* did not follow this same trend as *Q. rubra* is overall sample size. We only sampled one *Q. alba* and four *Q. macrocarpa* saplings across all of our plots, while 27 *Q. rubra* saplings were sampled.

Measures of *Rhamnus* were tested for edge and slope effects and edge effects alone. With slope included in the model, none of these measures were significant (Table 6). However, when only edge effects were considered, *Rhamnus* score ( $p < 0.01$ ) and *R. cathartica* sapling counts ( $p < 0.05$ ) were both significant (Table 7). Several factors need to be considered when deciding which of our statistical models to use when assessing edge effects and *Rhamnus* measures. Many invasive shrubs are known to be associated with microhabitats containing higher soil nutrients (Howard et al. 2004); however, our data indicate a positive association between *R. cathartica* and soil nutrients in interior forest positions, but no association with soil nutrients at the forest edge. For example, although the association is not significant at the  $p = 0.05$  level, we found that *Rhamnus* infestation was positively correlated with soil magnesium concentrations at distances of 45, 60, and 90 m from the forest edge (Figure 9); however, *Rhamnus* score is high and often highly variable at the edge despite relatively lower magnesium concentrations (Figures 8a,g and 9). We recorded a similar response for calcium concentration, total carbon, and total nitrogen.

Although classified as bird dispersed (Farrar 2001, Gill and Marks 1991), *R. cathartica* has been demonstrated to drop approximately 90% of its fruits directly beneath the canopy of mature shrubs (Archibold et al. 1997). Given this high percentage of seed rain, the steep slopes at our study site, and higher soil nutrients downslope, it might be expected that the level of *Rhamnus* infestation would be higher in our more interior sampling positions, as gravity and higher soil nutrients affected dispersal and shrub nutrient needs. Our findings (with slope excluded from our statistical model), however, show the opposite: *Rhamnus* scores are significantly higher at our 15 m plots when compared to our 90 m plots (Table 7, Figure 8g). This suggests that edge effects, and specifically increased light associated with edges, are more important than slope and soil nutrients in determining the distribution of *R. cathartica* within our study area. Other research supports this conclusion. Harrington et al. (1989) found that *R. cathartica* is able to better exploit light when compared to other common native shrub species, including *Cornus racemosa* and *Prunus serotina*. However, a variety of native and invasive shrubs consistently demonstrate a positive response to edge effects (Brothers and Spingarn 1992, Flory and Clay 2006, Honnay et al. 2002). It is also possible that our study has captured a snapshot of a progressing *R. cathartica* invasion. If *R. cathartica* invasion does begin at forest edges, it may take a number of decades before the interior of forests has been successfully invaded.

Regardless as to whether there is a slope and related nutrient effect or not, we found that levels of *Rhamnus* infestation and the number of *Q. rubra* saplings were both higher close to the forest edge, as compared to forest interior positions. This spatial arrangement places oak recruitment in direct competition with the known invasive shrub *R. cathartica*. *R. cathartica* is a successful competitor for light, as it exploits periods of high light by leafing

out earlier in the spring and retaining leaves later in the fall than native woody species (Harrington et al. 1989), and is also known to alter soil properties (Heneghan et al. 2004). For these reasons, it has demonstrated the ability to successfully infest many habitats including forests (Archibold et al. 1997, Czarapata 2005, Farrar 2001, Gill and Marks 1991). With the predominant oak species found within the region being relatively intolerant of shade (Jacobs and Wray 1992, Johnson et al. 2002), direct competition with this invasive shrub poses another threat to the future of oak forests in the region.

## CONCLUSIONS

Important implications for forest management in the Driftless Area, and perhaps Midwestern oak forests in general, can be drawn from this study. First and foremost, oak forests in this area appear to be converting to mesic, shade-tolerant species. Without significant efforts to improve oak species recruitment, it is very possible that oak species will lose their dominance as older oak trees are either harvested or experience mortality due to other factors. In addition, competition from the invasive shrub *R. cathartica* may negatively affect oak recruitment and management efforts especially on high light-high nutrient sites. This is of particular importance because oak species are already experiencing intense competition from shade tolerant species on low light, low nutrient, north facing slopes. We also found that levels of *Rhamnus* infestation and the number of *Q. rubra* saplings were both higher closer to the forest edges when compared to forest interiors. This spatial arrangement places current oak recruitment in direct competition with a known invasive shrub, *R. cathartica*, which is known to successfully infest many habitats including forests (Archibold

et al. 1997, Czarapata 2005, Farrar 2001, Gill and Marks 1991). Few, if any, areas without significant competition are thus available or suitable for oak recruitment.

Often forestry practitioners measure successful management of forests in terms of productivity, and not in terms of ecosystem sustainability (Shifley 2006). If managers and landowners wish to maintain oak forests in the Driftless Area, they need to undertake management practices that give oak species a competitive advantage over shade tolerant native species and invasive shrubs capable of competing in high light areas. Management practices could be altered to incorporate prescribed fire (Franklin et al. 2003, Hutchinson et al. 2005, Jacobs and Wray 2002, Lorimer et al. 1994) and, in the Midwest Driftless Area, to focus on upland edges and south-facing slopes. Without specific efforts to maintain oak species dominance, the future composition of oak forest habitats that have existed for over 5,000 years may be significantly altered (Fralish 2004).

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## TABLES AND FIGURES

Table 1. Tree species importance values (IV): means and standard deviations for 17 study sites.

Species	Abbreviation	Mean IV	Standard deviation
<i>Acer negundo</i> L.	acne	3.2	3.2
<i>Acer saccharum</i> Marsh.	acsa	2.0	4.7
<i>Amelanchier arborea</i> (Michaux f.) Fernald	amar	0.0	0.1
<i>Betula papyrifera</i> Marsh.	bepa	3.7	5.4
<i>Carya cordiformis</i> (Wangenh.) K. Koch	caco	0.2	0.6
<i>Carya ovata</i> (Mill.) K. Koch	caov	0.5	1.3
<i>Celtis occidentalis</i> L.	ceoc	2.4	2.6
<i>Crataegus</i> spp.	crat	0.0	0.1
<i>Fraxinus americana</i> L.	fram	0.8	1.9
<i>Fraxinus nigra</i> Marsh.	frni	0.0	0.2
<i>Juglans nigra</i> L.	juni	1.6	3.2
<i>Juniperus virginiana</i> L.	juvi	0.2	0.6
<i>Ostrya virginiana</i> (Mill.) K. Koch	osvi	3.1	4.6
<i>Pinus resinosa</i> Ait.	pire	0.4	1.2
<i>Populus deltoides</i> Bartr. ex Marsh.	pode	0.7	2.7
<i>Populus tremuloides</i> Michx.	potr	4.5	7.7
<i>Prunus pensylvanica</i> L. f.	prpe	0.0	0.2
<i>Prunus serotina</i> Ehrh.	prse	1.7	1.8
<i>Quercus alba</i> L.	qual	5.0	6.1
<i>Quercus ellipsoidalis</i> E.J. Hill	quel	0.4	1.0
<i>Quercus macrocarpa</i> Michx.	quma	14.8	16.7
<i>Quercus palustris</i> Muenchh.	qupa	0.4	1.6
<i>Quercus rubra</i> L.	quru	30.5	15.2
<i>Quercus velutina</i> Lam.	quve	0.9	2.5
<i>Robinia pseudoacacia</i> L.	rops	0.1	0.4
<i>Tilia americana</i> L.	tiam	6.3	7.0
<i>Ulmus americana</i> L.	ulam	16.3	11.7

Table 2. Summary statistics from vector fitting environmental variables to the non-metric multidimensional scaling analysis (NMDS) of the tree community.

Variable	Abbreviation	R <sup>2</sup>	<i>p</i> -value
Tree basal area	tb	0.70	<0.01
pH	ph	0.61	<0.01
<i>Rhamnus</i> score	rs	0.72	<0.01
Potassium	k	0.58	<0.01
Calcium	c	0.53	<0.01
Total nitrogen	tn	0.39	<0.05
Total carbon	tc	0.38	<0.05
Magnesium	m	0.35	<0.05
Sodium	n	0.34	0.06
Heat load index	hli	0.28	0.10
<i>Lonicera</i> score	ls	0.17	0.26
Canopy cover	cc	0.15	0.32
Bulk density	bd	0.04	0.77
Slope	sl	0.03	0.83

Table 3. Graph coordinates from vector fitting significant ( $p < 0.05$ ) environmental variables to the non-metric multidimensional scaling analysis (NMDS) of the tree community.

	Abbreviation	NMDS1	NMDS2
Tree			
<i>Acer negundo</i>	acne	-0.14	-0.19
<i>A. saccharum</i>	acsa	0.89	0.36
<i>Amelanchier arborea</i>	amar	0.38	0.72
<i>Betula papyrifera</i>	bepa	0.35	-0.59
<i>Carya cordiformis</i>	caco	-0.05	0.25
<i>C. ovata</i>	caov	-0.42	0.07
<i>Celtis occidentalis</i>	ceoc	-0.49	-0.10
<i>Crataegus</i> spp.	crat	1.24	-0.12
<i>Fraxinus americana</i>	fram	0.72	0.80
<i>F. nigra</i>	frni	0.52	0.17
<i>Juglans nigra</i>	juni	-0.21	0.12
<i>Juniperus virginiana</i>	juvi	-0.95	-0.68
<i>Ostrya virginiana</i>	osvi	0.82	0.18
<i>Pinus resinosa</i>	pire	0.91	-0.43
<i>Populus deltoides</i>	pode	-0.92	-0.62
<i>Populus tremuloides</i>	potr	-0.54	-0.02
<i>Prunus pensylvanica</i>	prpe	0.15	-1.16
<i>Prunus serotina</i>	prse	-0.02	-0.10
<i>Quercus alba</i>	qual	0.68	0.00
<i>Q. ellipsoidalis</i>	quel	0.39	-0.60
<i>Q. macrocarpa</i>	quma	-0.70	0.35
<i>Q. palustris</i>	qupa	-1.40	1.23
<i>Q. rubra</i>	quru	0.29	0.12
<i>Q. velutina</i>	quve	1.00	0.11
<i>Robinia pseudoacacia</i>	rops	-0.62	-0.22
<i>Tilia americana</i>	tiam	-0.18	-0.15
<i>Ulmus americana</i>	ulam	-0.15	-0.39
Environmental vectors			
Calcium	c	-1.00	-0.02
Potassium	k	-0.79	0.61
Magnesium	m	-0.75	0.67
pH	ph	-1.00	0.06
<i>Rhamnus</i> score	rs	-0.91	-0.41
Tree basal area	tb	0.60	0.80
Total carbon	tc	-0.98	-0.18
Total nitrogen	tn	-1.00	-0.06

Table 4. Summary statistics from vector fitting environmental variables to the non-metric multidimensional scaling (NMDS) analysis of the plant community.

Variable	Abbreviation	R <sup>2</sup>	<i>p</i> -value
<i>Rhamnus</i> score	rs	0.751	<0.01
Tree basal area	tb	0.660	<0.01
pH	ph	0.607	<0.01
Calcium	c	0.389	<0.05
Total nitrogen	tn	0.339	<0.05
Total carbon	tc	0.309	0.07
Potassium	k	0.310	0.08
<i>Lonicera</i> score	ls	0.283	0.10
Canopy cover	cc	0.268	0.10
Magnesium	m	0.238	0.16
Heat load index	hli	0.120	0.45
Bulk density	bd	0.097	0.49
Slope	sl	0.004	0.97
Sodium	n	0.002	0.99

Table 5. Graph coordinates from vector fitting significant ( $p < 0.05$ ) environmental variables to the non-metric multidimensional scaling (NMDS) analysis of the plant community.

	Abbreviation	NMDS1	NMDS2
Trees			
<i>Quercus alba</i>	qual	-0.62	0.06
<i>Q. macrocarpa</i>	quma	0.49	-0.20
<i>Q. rubra</i>	quru	-0.36	0.03
<i>Tilia americana</i>	tiam	0.10	0.12
<i>Ulmus americana</i>	ulam	0.15	0.26
Saplings			
<i>Acer negundo</i>	acnep	-0.08	0.39
<i>A. saccharum</i>	acsap	-1.55	-0.70
<i>Celtis occidentalis</i>	ceocp	0.23	0.34
<i>Ostrya virginiana</i>	osvip	-0.62	-0.11
<i>Prunus serotina</i>	prsep	0.46	-0.04
<i>Rhamnus cathartica</i>	rhcaph	0.81	-0.21
<i>T. americana</i>	tiamp	-0.25	0.22
<i>U. americana</i>	ulamp	-0.06	0.24
Shrubs			
<i>Ribes</i> spp.	ribesh	0.19	0.18
<i>R. cathartica</i>	rhcash	0.86	-0.61
<i>Cornus</i> spp.	cornsh	0.27	-0.28
<i>P. serotina</i>	prsesh	0.18	-0.06
<i>P. virginiana</i>	prvish	-0.16	-0.02
<i>U. americana</i>	ulamsh	-0.28	0.01
<i>Zanthoxylum americanum</i>	zaamsh	0.45	-0.59
Environmental vectors			
Calcium	c	0.99	-0.11
pH	ph	0.67	-0.74
Total nitrogen	tn	0.98	0.22
Tree basal area	tb	-0.94	-0.35
<i>Rhamnus</i> score	rs	0.89	-0.45

Table 6. Results of test for differences in environmental and vegetation metrics with distance from edge; slope was also included as an explanatory variable due to potential confounding.

Metric	Plot 1 (15-m)			Plot 2 (40-m)			Plot 3 (65-m)			Plot 4 (90-m)		Overall <i>p</i> -value	Slope <i>p</i> -value
	Mean	SE <sup>2</sup>	<i>P</i> -value <sup>1</sup>	Mean	SE <sup>2</sup>	<i>P</i> -value <sup>1</sup>	Mean	SE <sup>2</sup>	<i>P</i> -value <sup>1</sup>	Mean	SE <sup>2</sup>		
Environmental metric:													
Percent total Carbon	3.36	0.09	<0.01	4.34	0.22	0.22	4.47	0.23	0.16	5.00	0.36	<0.05	<0.05
Percent total Nitrogen	0.27	0.01	<0.05	0.33	0.01	0.68	0.34	0.02	0.52	0.36	0.02	0.07	<0.05
Calcium (ppm)	2235	83	0.18	2668	141	0.59	2718	166	0.27	2978	156	0.45	<0.01
Magnesium (ppm)	352	11.6	<0.01	463	32	<0.01	542	34	<0.05	627	35	<0.01	<0.01
Potassium (ppm)	132	6.0	0.52	171	11.2	0.13	164	9.33	0.79	168	8.98	0.08	<0.01
Sodium (ppm)	7.90	0.63	0.75	7.89	0.48	0.30	8.51	0.56	0.58	9.08	0.73	0.75	0.13
pH	6.30	0.06	0.59	6.43	0.08	0.66	6.43	0.10	0.29	6.57	0.09	0.76	<0.05
Vegetation metric:													
Tree basal area (m <sup>2</sup> /ha)	25.32	2.29	<0.01	23.19	2.03	<0.01	19.72	1.64	0.12	16.14	1.39	<0.01	0.38
<i>Quercus alba</i> IV <sup>2</sup>	1.48	0.64	0.82	1.35	0.73	0.85	0.94	0.37	0.95	1.94	0.59	1.00	0.13
<i>Q. macrocarpa</i> IV <sup>2</sup>	4.19	1.08	0.35	3.51	0.97	0.73	3.02	0.86	0.94	2.61	0.65	0.78	0.45
<i>Q. rubra</i> IV <sup>2</sup>	10.16	2.09	0.77	9.42	1.91	0.39	9.48	1.77	0.78	8.07	1.40	0.85	0.49
<i>Acer saccharum</i> (sap <sup>2</sup> /ha)	4.17	3.08	<0.05	27.78	15.4	0.09	30.56	13.2	0.07	62.50	27.6	0.53	0.13
<i>Ostrya virginiana</i> (sap <sup>2</sup> /ha)	26.39	8.82	<0.05	52.78	18.1	0.18	69.44	18.6	0.50	81.94	23.1	0.23	0.83
<i>Q. alba</i> (sap <sup>2</sup> /ha)	0.00	0.00	0.77	0.00	0.00	0.88	1.39	1.39	0.14	0.00	0.00	0.44	0.55
<i>Q. macrocarpa</i> (sap <sup>2</sup> /ha)	1.39	1.39	0.39	1.39	1.39	0.65	2.78	2.78	0.75	1.39	1.39	0.66	0.08
<i>Q. rubra</i> (sap <sup>2</sup> /ha)	26.39	7.36	<0.01	5.56	3.34	0.58	4.17	3.08	0.69	1.39	1.39	<0.01	0.72
<i>Rhamnus cathartica</i> (sap <sup>2</sup> /ha)	75.00	33	0.20	31.94	11.6	0.81	18.06	9.26	0.91	16.67	9.42	0.49	0.28
<i>R. cathartica</i> (shrubs/ha)	1062	345	0.46	292	89	0.30	1146	431	0.15	604	183	0.07	0.64
<i>R. cathartica</i> diam <sup>2</sup> (cm)	2.68	0.52	0.20	1.70	0.37	0.71	1.54	0.30	0.51	1.71	0.37	0.21	0.37
<i>Rhamnus</i> score	0.88	0.15	0.44	0.54	0.09	0.41	0.69	0.12	0.48	0.56	0.11	0.17	0.11
<i>Lonicera</i> score	0.40	0.09	0.54	0.19	0.08	0.45	0.21	0.08	0.63	0.25	0.09	0.48	0.49

<sup>1</sup>Plots 1, 2, and 3 are compared to Plot 4, the interior-most plot and baseline for this comparison.

<sup>2</sup>SE = standard error; IV = importance value; sap = saplings; diam = diameter.

Table 7. Results of test for differences in environmental and vegetation metrics with distance from edge; slope not included as an explanatory variable.

Metric	Plot 1 (15-m)			Plot 2 (40-m)			Plot 3 (65-m)			Plot 4 (90-m) <sup>1</sup>		Overall <i>p</i> -value
	Mean	SE <sup>2</sup>	<i>p</i> -value	Mean	SE <sup>2</sup>	<i>p</i> -value	Mean	SE <sup>2</sup>	<i>p</i> -value	Mean	SE <sup>2</sup>	
Environmental metric:												
Slope	10.72	0.63	<0.01	16.60	1.06	<0.01	19.43	1.05	<0.01	21.67	1.14	<0.01
Percent total Carbon	3.36	0.09	<0.01	4.34	0.22	<0.05	4.47	0.23	0.07	5.00	0.36	<0.01
Percent total Nitrogen	0.27	0.01	<0.01	0.33	0.01	0.23	0.34	0.02	0.31	0.36	0.02	<0.01
Calcium (ppm)	2235	84	<0.01	2668	141	0.06	2718	166	0.09	2978	156	<0.01
Magnesium (ppm)	352	11.6	<0.01	463	32	<0.01	542	34	<0.01	627	35	<0.01
Potassium (ppm)	132	5.96	<0.01	171	11.2	0.75	164	9.33	0.72	168	8.98	<0.01
Sodium (ppm)	7.90	0.63	0.09	7.89	0.48	0.09	8.51	0.56	0.41	9.08	0.73	0.27
pH	6.30	0.06	<0.01	6.43	0.08	0.18	6.43	0.10	0.15	6.57	0.09	0.07
Vegetation metric:												
Tree basal area (m <sup>2</sup> /ha)	25.32	2.29	<0.01	23.19	2.03	<0.01	19.72	1.64	0.15	16.14	1.39	<0.01
<i>Quercus alba</i> IV <sup>2</sup>	1.48	0.64	0.59	1.35	0.73	0.99	0.94	0.37	0.82	1.94	0.59	0.91
<i>Q. macrocarpa</i> IV <sup>2</sup>	4.19	1.08	0.09	3.51	0.97	0.58	3.02	0.86	0.91	2.61	0.65	0.30
<i>Q. rubra</i> IV <sup>2</sup>	10.16	2.09	0.89	9.42	1.91	0.49	9.48	1.77	0.86	8.07	1.40	0.85
<i>Acer saccharum</i> (sap <sup>2</sup> /ha)	4.17	3.08	<0.01	27.78	15.4	<0.05	30.56	13.2	0.05	62.50	28	<0.01
<i>Ostrya virginiana</i> (sap <sup>2</sup> /ha)	26.39	8.82	<0.01	52.78	18.1	0.12	69.44	18.6	0.46	81.94	23	<0.05
<i>Q. alba</i> (sap <sup>2</sup> /ha)	0.00	0.00	1.00	0.00	0.00	1.00	1.39	1.39	0.16	0.00	0.00	0.39
<i>Q. macrocarpa</i> (sap <sup>2</sup> /ha)	1.39	1.39	1.00	1.39	1.39	1.00	2.78	2.78	0.60	1.39	1.39	0.94
<i>Q. rubra</i> (sap <sup>2</sup> /ha)	26.39	7.36	<0.01	5.56	3.34	0.49	4.17	3.08	0.65	1.39	1.39	<0.01
<i>Rhamnus cathartica</i> (sap <sup>2</sup> /ha)	75.00	33	<0.05	31.94	11.6	0.52	18.06	9.26	0.95	16.67	9.42	<0.05
<i>R. cathartica</i> (shrubs/ha)	1062	345	0.19	292	89	0.34	1146	431	0.12	604	183	0.06
<i>R. cathartica</i> diam (cm)	2.68	0.52	0.07	1.70	0.37	0.83	1.54	0.30	0.43	1.71	0.37	0.09
<i>Rhamnus</i> score	0.88	0.15	<0.01	0.54	0.09	0.84	0.69	0.12	0.29	0.56	0.11	<0.01
<i>Lonicera</i> score	0.40	0.09	0.18	0.19	0.08	0.57	0.21	0.08	0.70	0.25	0.09	0.22

<sup>1</sup>No *p*-value is reported for Plot 4, the interior-most plot, because it is treated as a baseline to which Plots 1, 2, and 3 are compared.

<sup>2</sup>SE = standard error; IV = importance value; sap = saplings; diam = diameter.

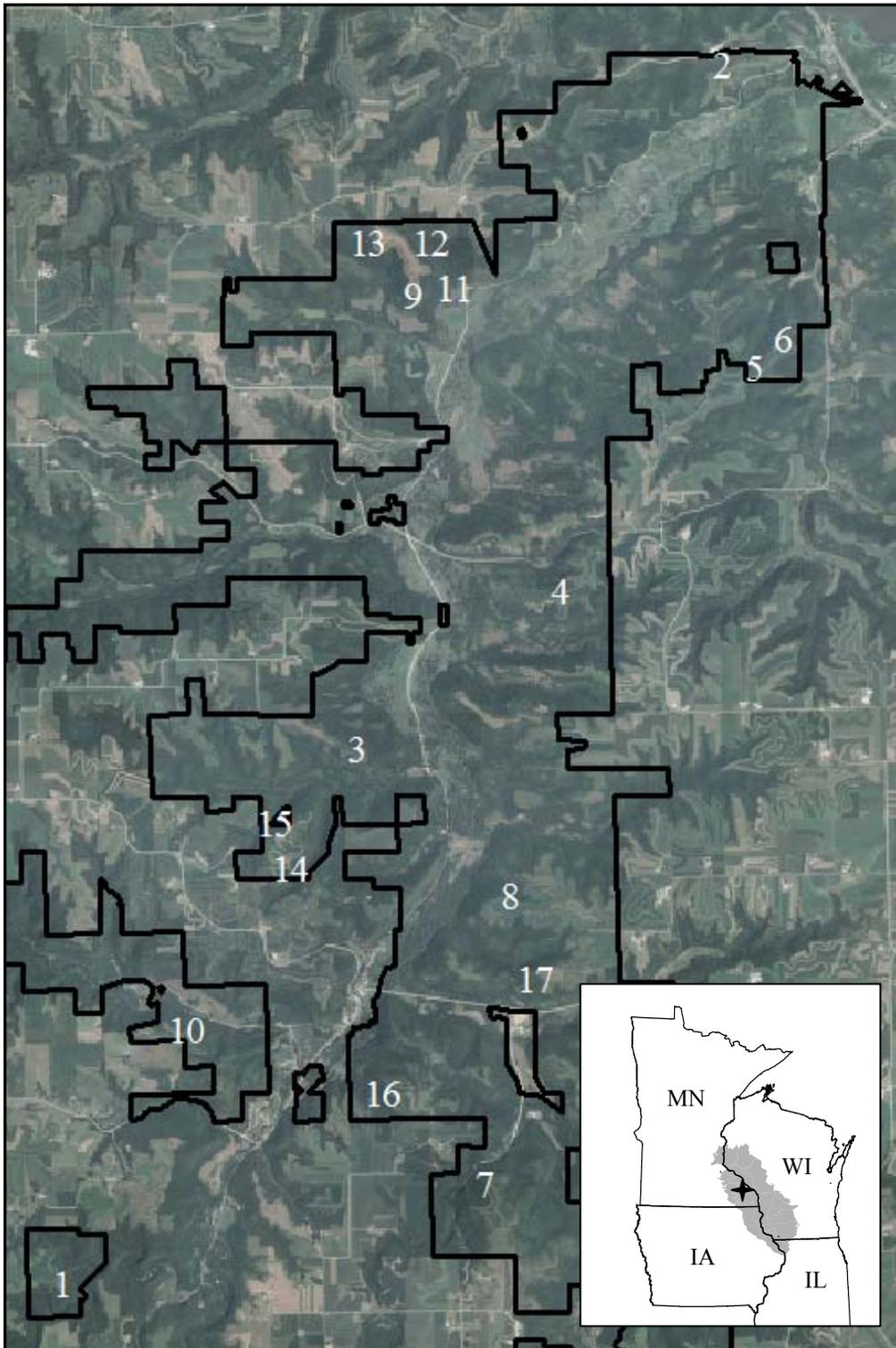


Figure 1. Location of 17 study sites within the Whitewater Wildlife Management Area of southeastern Minnesota, USA. Inset: the location of Whitewater Wildlife Management Area within the Midwest Driftless Area (shaded) and the upper Midwest region.

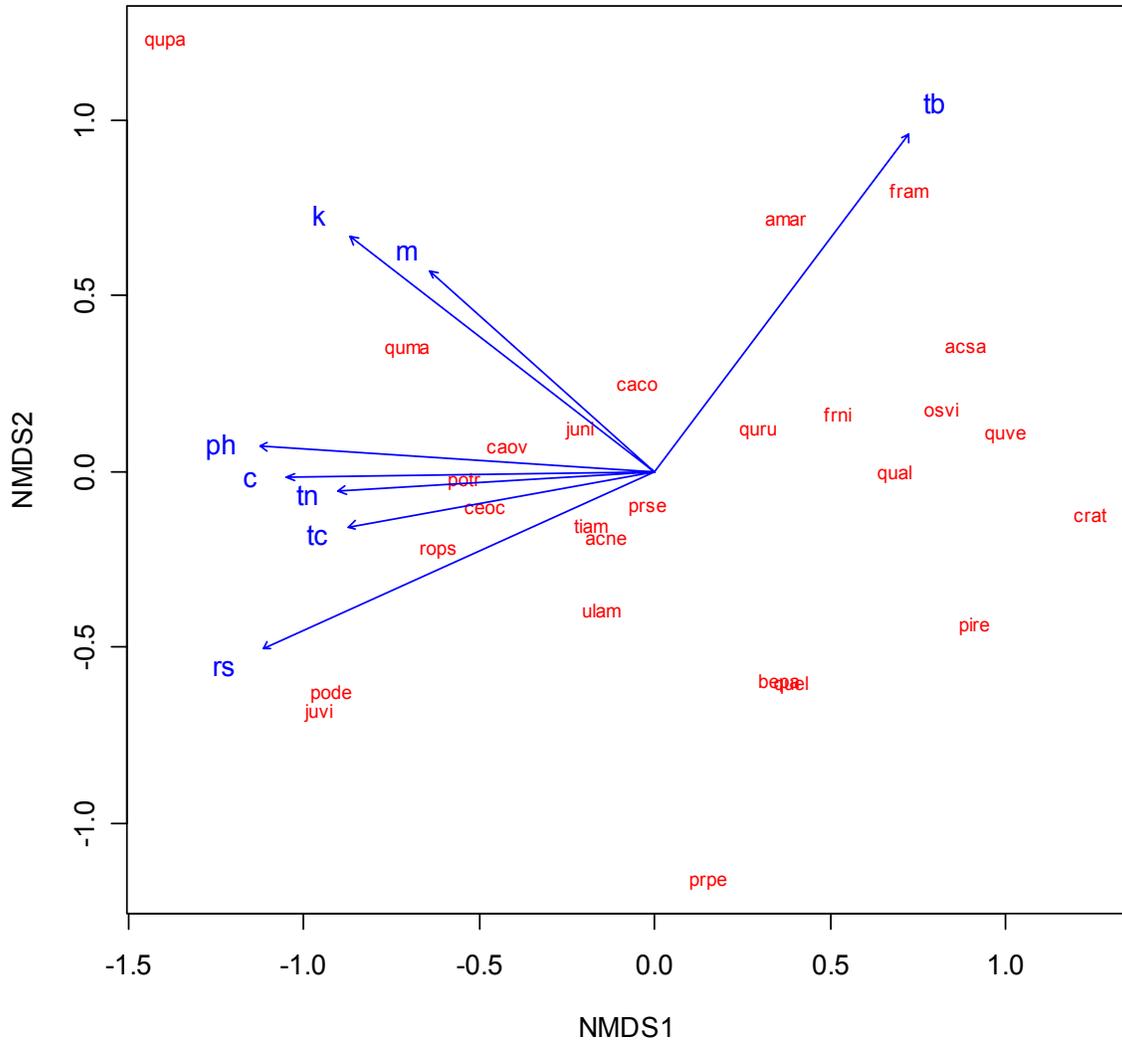


Figure 2. Axis 1 and 2 results of non-metric multidimensional scaling (NMDS) tree community analysis; environmental vectors significant to  $p=0.05$  shown. Abbreviations for vegetation and environmental variables are found in Table 3.

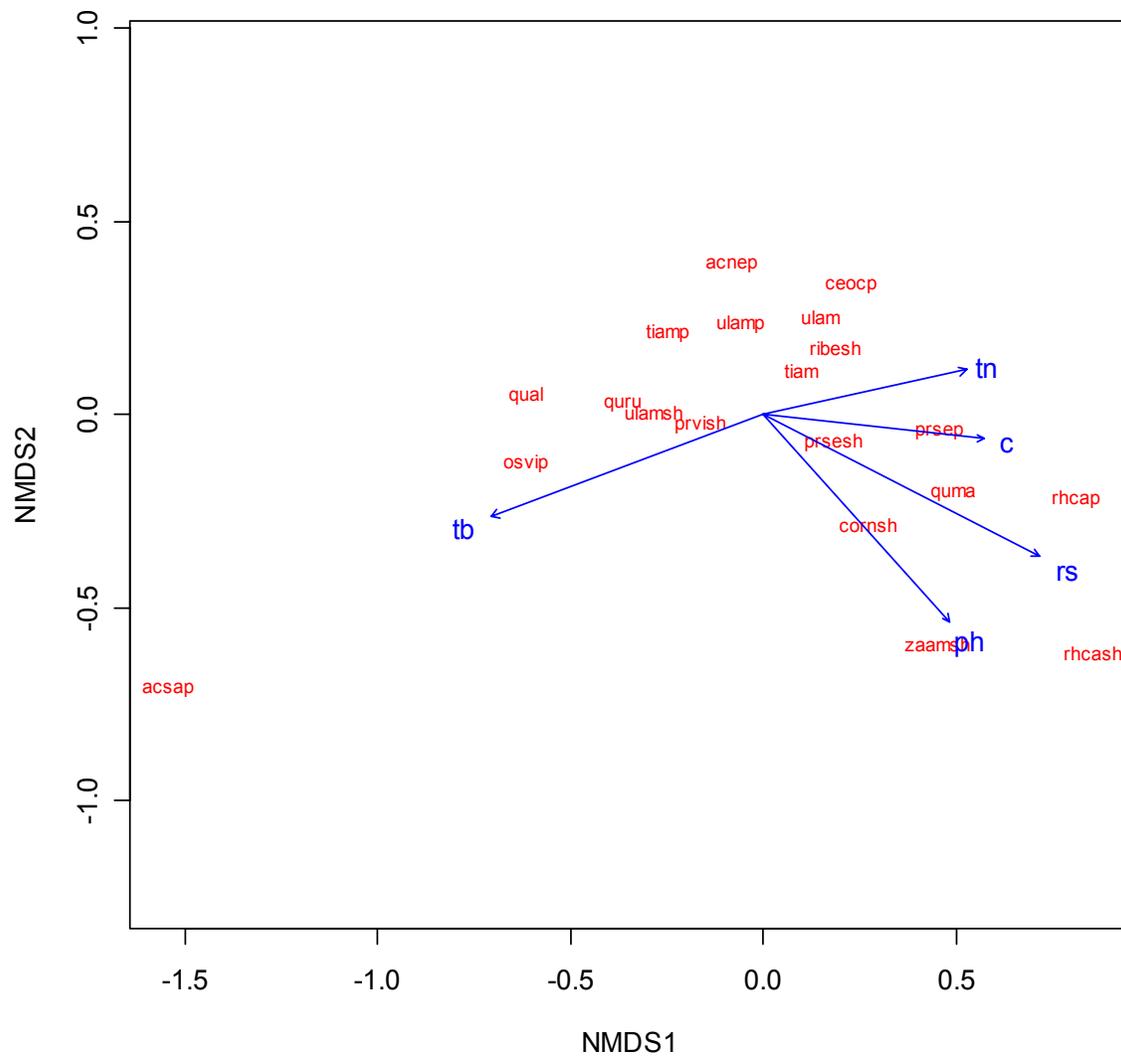


Figure 3. Axis 1 and 2 results of non-metric multidimensional scaling (NMDS) plant community analysis; environmental vectors significant to  $p=0.05$  shown. Abbreviations for vegetation and environmental variables are found in Table 5.

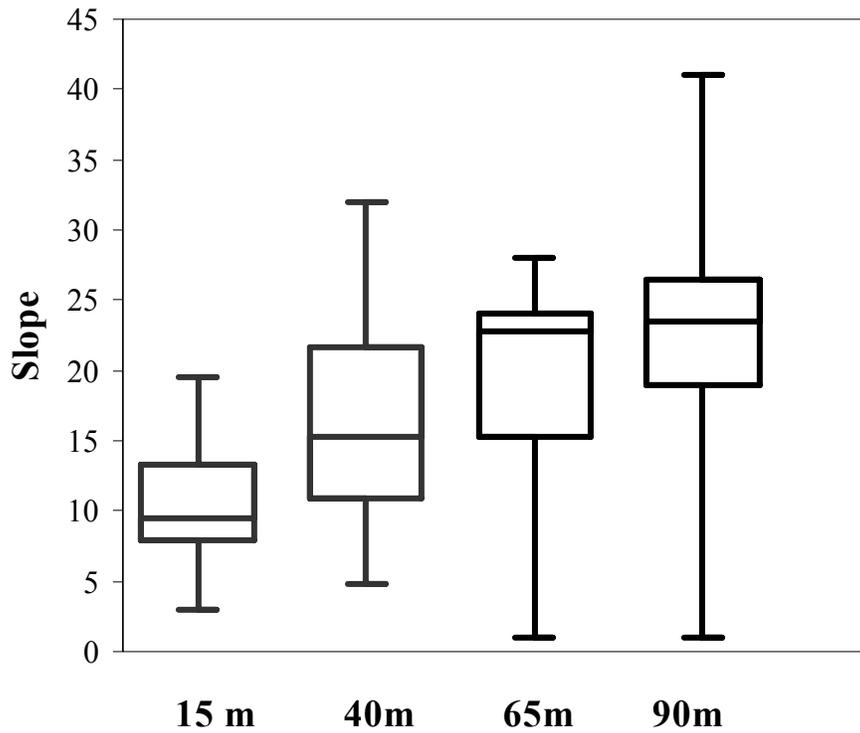


Figure 4. Boxplots for topographic slope by distance to forest edge. Box lengths represent an interquartile range from the 25<sup>th</sup> to the 75<sup>th</sup> percentile, the horizontal line within each box represents the median value, and the vertical lines issuing from each box extend to minimum and maximum values.

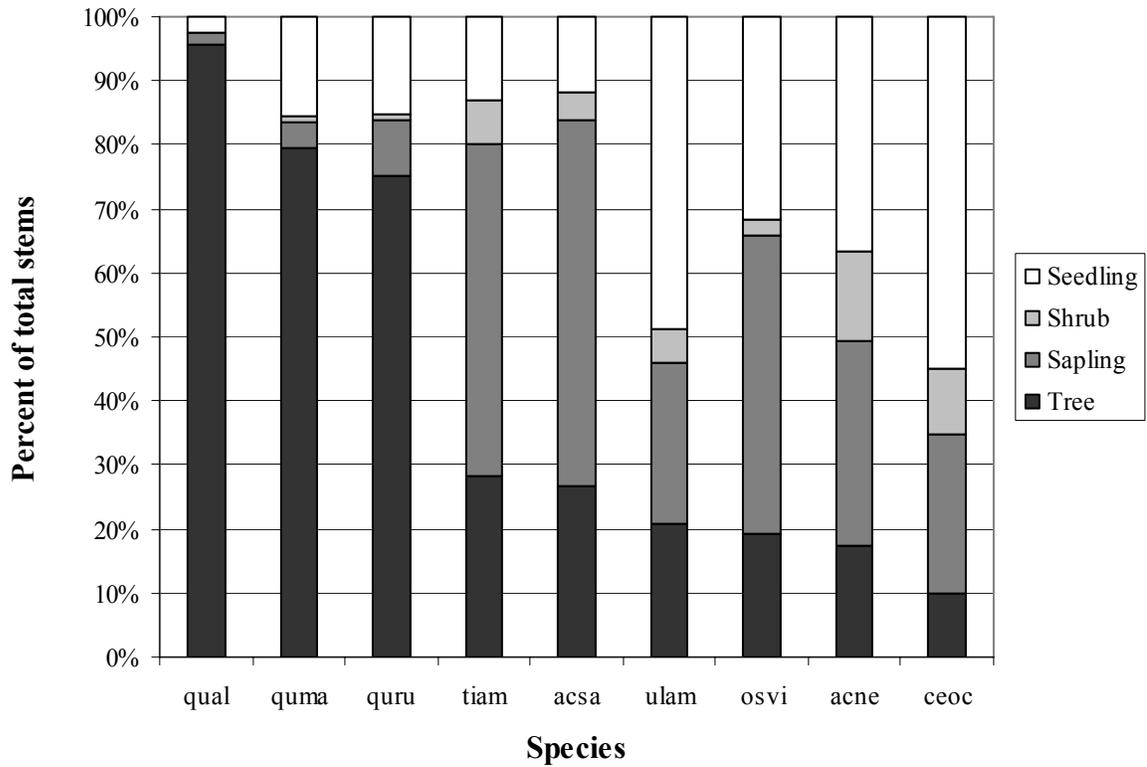
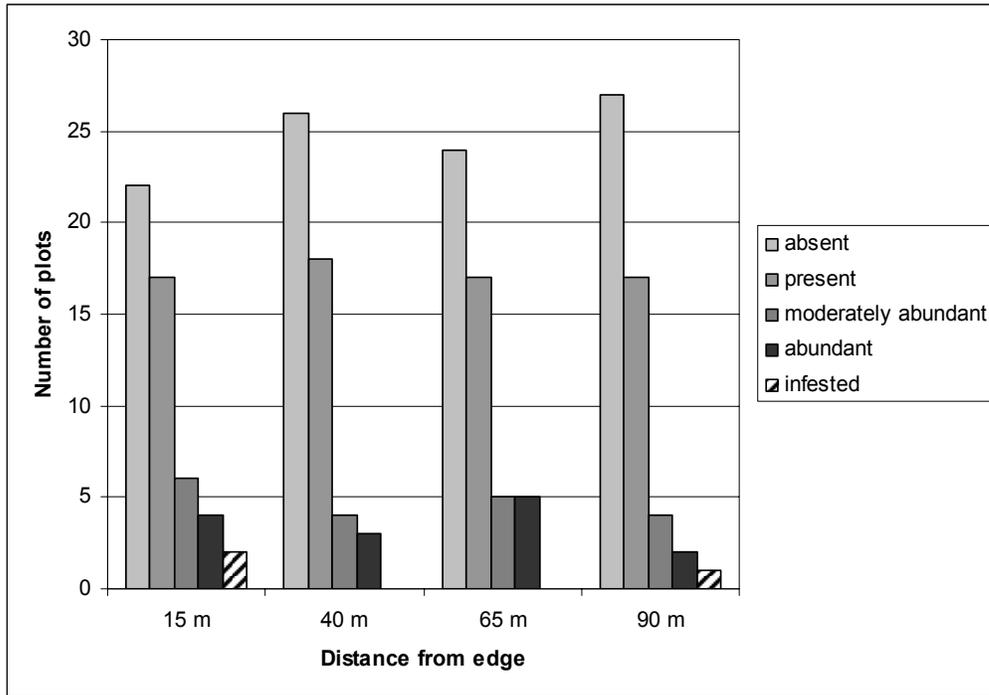
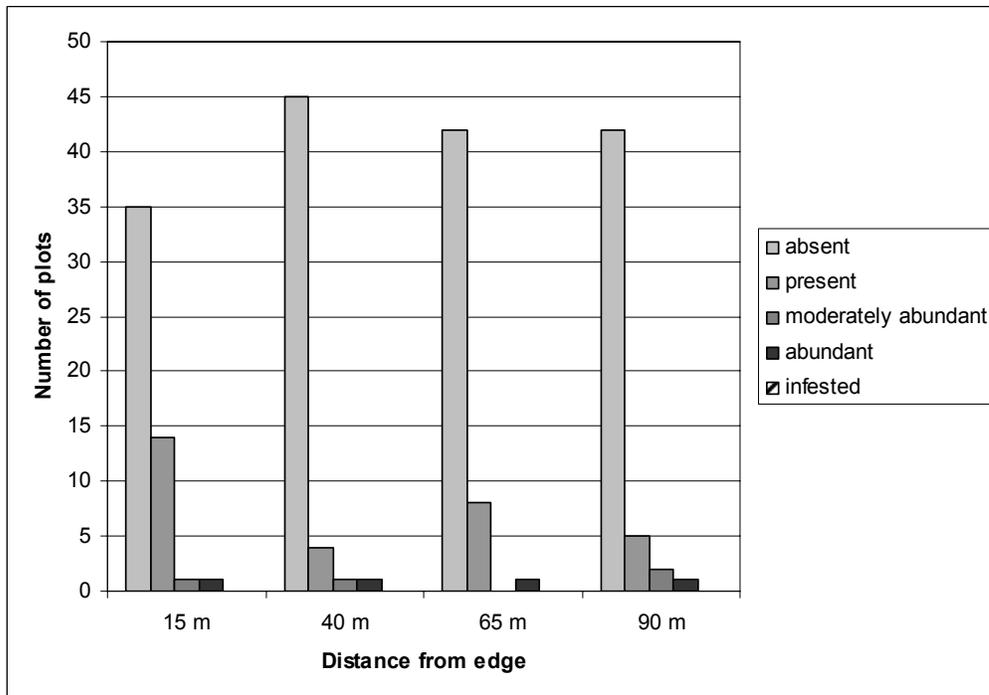


Figure 5. Percent of stems within each vegetation layer (tree, sapling, shrub, and seedling) for predominant tree species: *Quercus alba* (qual), *Q. macrocarpa* (quma), *Q. rubra* (quru), *Tilia americana* (tiam), *Acer saccharum* (acsa), *Ulmus americana* (ulam), *Ostrya virginiana* (osvi), *A. negundo* (acne), and *Celtis occidentalis* (ceoc).

a) *Rhamnus* scoreb) *Lonicera* scoreFigure 6. Frequency and distributions of (a) *Rhamnus* and (b) *Lonicera* scores.

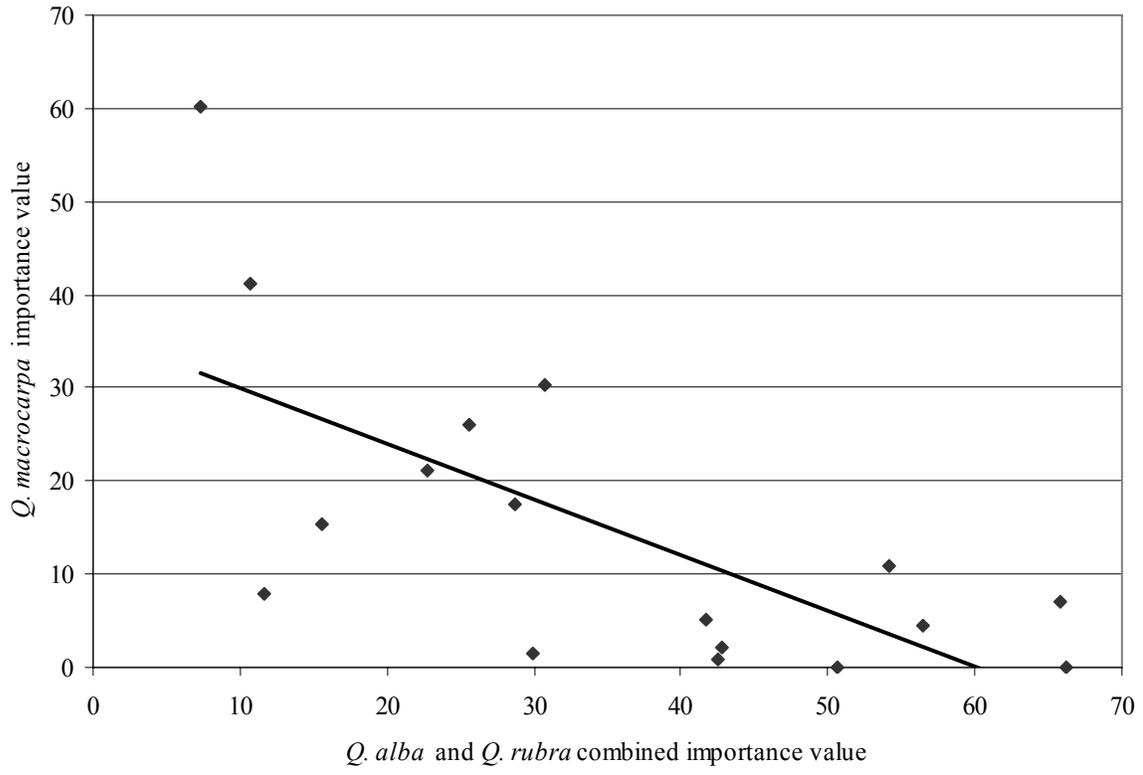


Figure 7. Relationship between mean *Quercus macrocarpa* importance value to the mean value of *Q. alba* and *Q. rubra* combined by study site. Linear trend line also shown ( $R^2=0.46$ ).

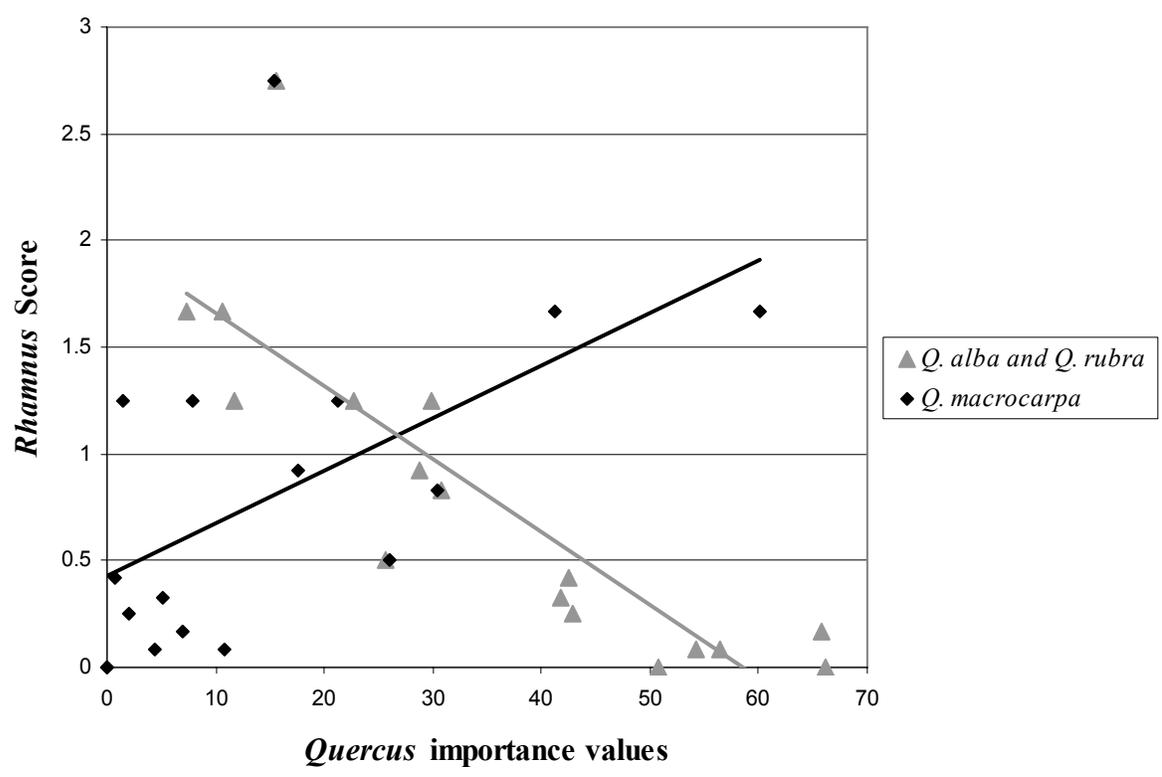


Figure 8. Relationship between mean *Rhamnus* score (0=absent, 1=present, 2=moderately abundant, 3=abundant, and 4=infested) and mean *Quercus* importance values by study site. Linear trend lines fitted for *Q. alba* and *Q. rubra* combination ( $R^2=0.71$ ) and *Q. macrocarpa* ( $R^2=0.29$ ) shown.

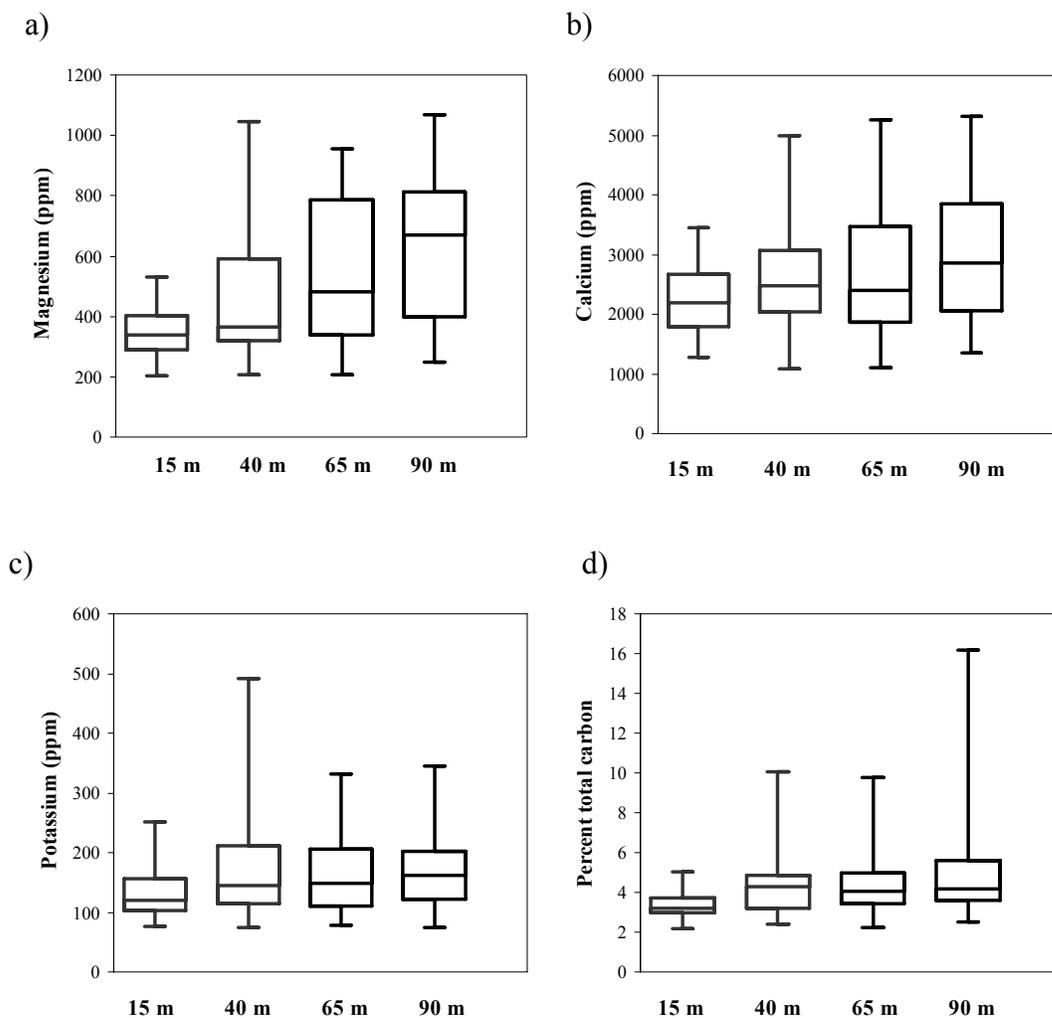
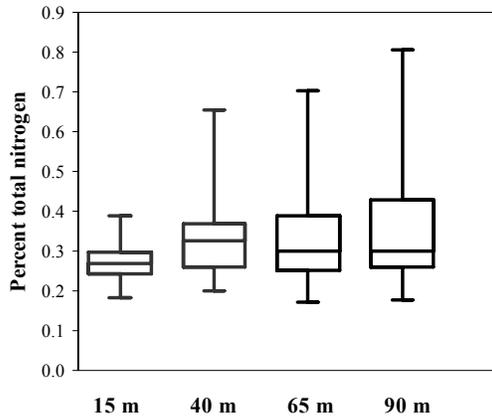


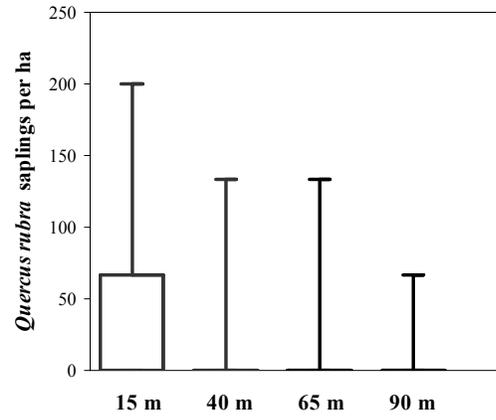
Figure 9. Boxplots for environmental and vegetation variables demonstrating significant ( $p \leq 0.05$ ) differences based on distance to forest edge: (a) soil magnesium, (b) soil calcium, (c) soil potassium, (d) total soil carbon, (e) total soil nitrogen, (f) *Quercus rubra* saplings, (g) *Rhamnus* score (0=absent, 1=present, 2=moderately abundant, 3=abundant, and 4=infested), (h) *R. cathartica* saplings, (i) *Acer saccharum* saplings, (j) *Ostrya virginiana* saplings, and (k) tree basal area. Examples of non significant ( $p \geq 0.05$ ) differences based on distance to forest edge are (l) *Quercus macrocarpa* importance value and (m) *Q. rubra* importance value. Box lengths represent an interquartile range from the 25<sup>th</sup> to the 75<sup>th</sup> percentile, the horizontal line within each box represents the median value, and the vertical lines issuing from each box extend to minimum and maximum values for each variable.

Figure 9. Continued.

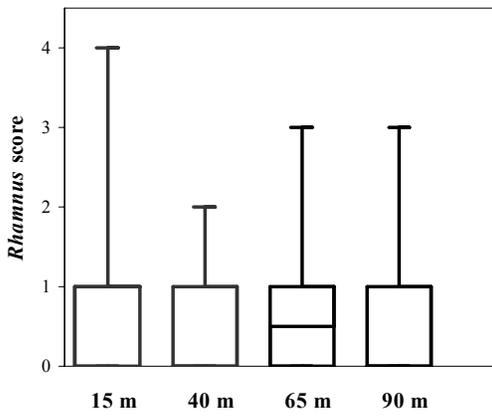
e)



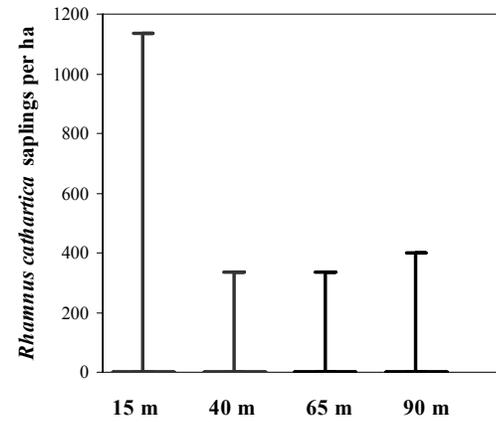
f)



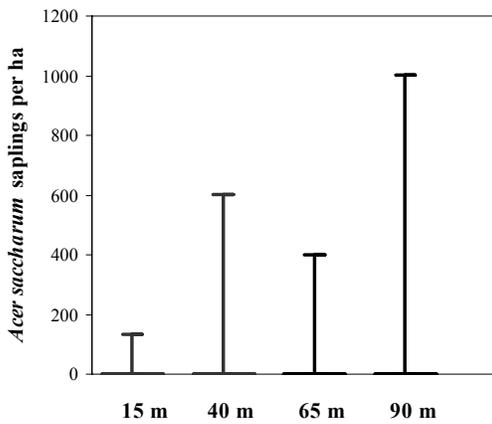
g)



h)



i)



j)

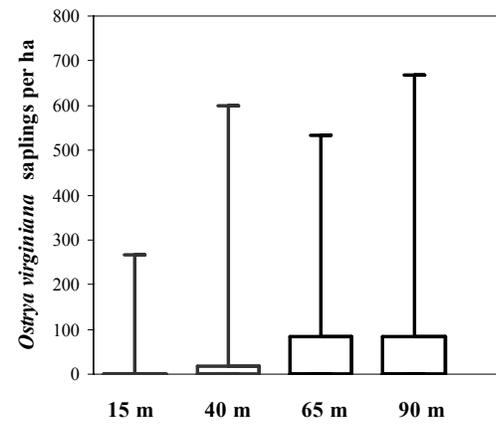
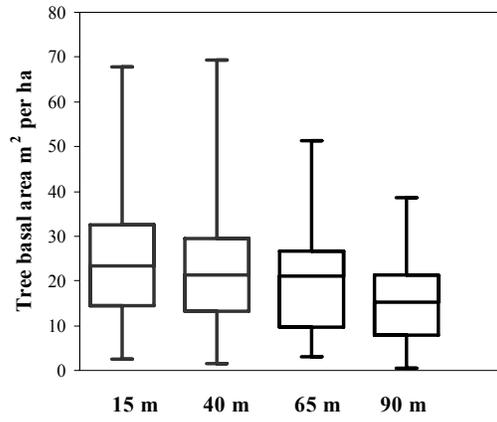
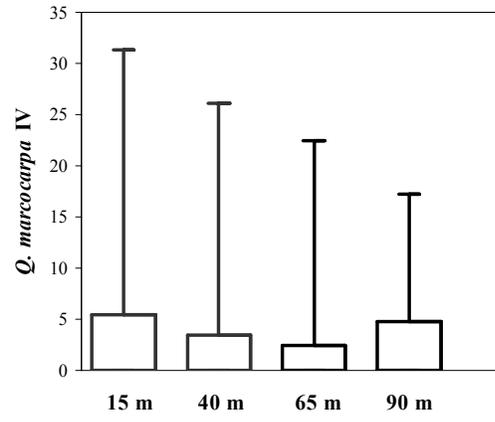


Figure 9. Continued.

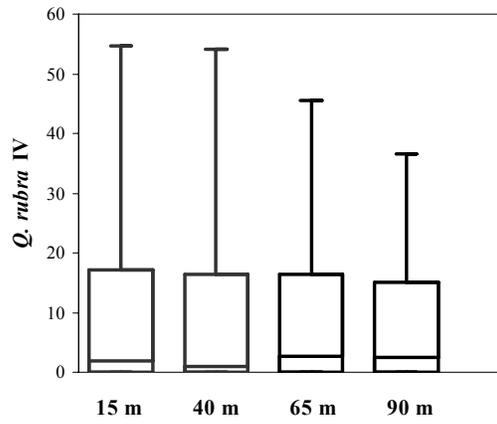
k)



l)



m)



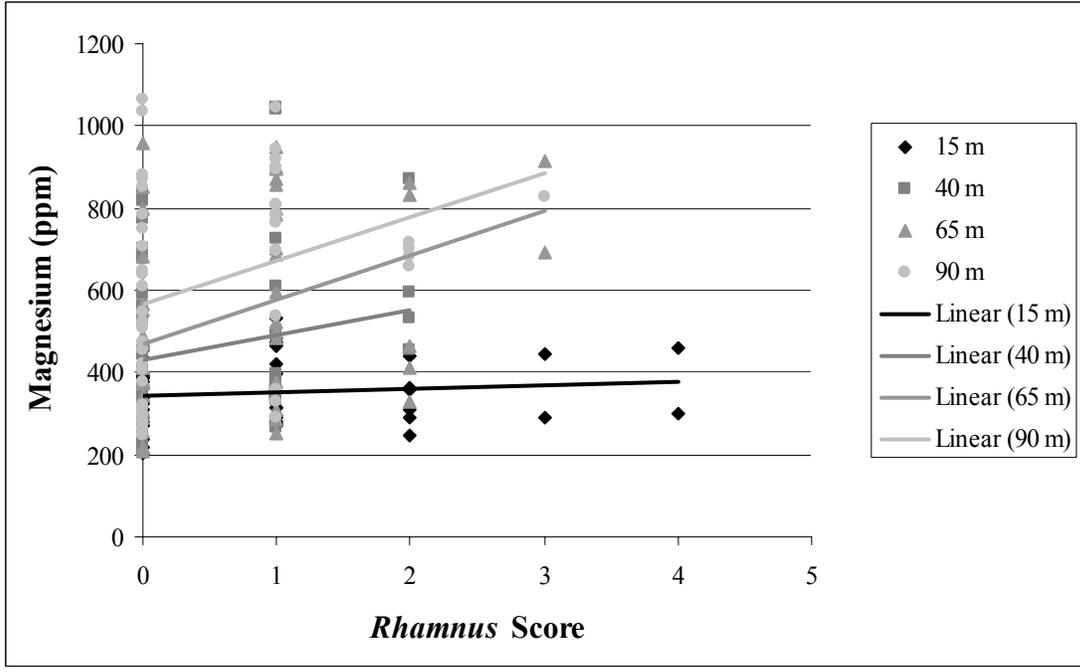


Figure 10. Relationship between soil magnesium concentration and *Rhamnus* score (0=absent, 1=present, 2=moderately abundant, 3=abundant, and 4=infested) according to distance from edge (15, 40, 65, and 90 m). Trend lines are not significant at the  $p = 0.05$  level;  $R^2 < 0.15$  for all four distances. Similar trends were observed with calcium concentrations, total soil carbon, and total soil nitrogen.

## CHAPTER 3.

### GENERAL CONCLUSIONS

#### **Current status of oak forest**

Oak (*Quercus*) forests across the United States are known to be undergoing dramatic changes (Abrams 2003, Kessler 1992, Pallardy et al. 1988, Shotola et al. 1992, Roovers and Shifley 2003). While concern over oak forest decline has continued to grow, causal factors remain difficult to elucidate (Abrams 2003, Jacobs and Wray 2002, Lorimer 2003).

Here I reveal a forest composition that typifies oak forest decline in the Midwest Driftless Area. In the forest stands that I worked in, oak species are highly underrepresented in all vegetation layers but the tree canopy. As these mature oak trees die or are harvested for timber, there are few oak recruits to successfully compete and maintain an oak dominated forest. The low number of oak recruits and relatively high number of non-oak recruits concurs with other studies on declining oak forest (Abrams 2003, Lorimer et al. 1994, Pallardy et al. 1988, Pierce et al. 2006, Shotola et al. 1992). If oak forest decline continues to occur in these areas, the changes in tree stand composition may have significant impacts on a multitude of other flora and fauna (Fralish 2004, Rodewald and Abrams 2002).

#### **Impacts of invasive shrubs in oak forests**

Based on my findings, it does not appear that *L. tartarica* is currently posing a direct threat to intact oak forests. *L. tartarica* was sampled in low, infrequent numbers; I found *L. tartarica* on only 39 of the 204 plots I sampled, with only eight of these plots having more than a few shrubs. However, I anecdotally noted the presence of *L. tartarica* in frequently

high light environments nearby my study sites, including the extreme outer edges of oak forests adjacent to agricultural lands and in areas that did not have a significant closed forest canopy. The presence of these shrubs might pose a constraint to oak establishment in these areas if such is a desired management goal.

*R. cathartica* was found in over half of our study plots and demonstrated an affinity for edge conditions. It is unclear, based on the results of my study, whether *R. cathartica* populations are demonstrating a lag-phase type of invasion, slowly creeping in from the forest edge, or if the species will be unable to successfully invade further into these forests. Currently, *R. cathartica* is most prevalent in areas that have the highest oak recruitment to sapling size, suggesting potential competition between *R. cathartica* and oak recruitment in these areas. *R. cathartica* was also found in association with *Q. macrocarpa*; both *R. cathartica* and *Q. macrocarpa* were disassociated with *Q. alba* and *Q. rubra*. This is a novel finding from my study and might aid managers in targeting effort on oak forest regeneration and *R. cathartica* control. Forest stand inventories listing *Q. macrocarpa* as the primary species could alert managers to the potential for high *R. cathartica* infestations. Additionally, since many cool and moist north-facing oak forests are being replaced with mesic species such as *A. saccharum*, some forest managers have opted to focus on maintaining oak forests on warmer, drier south-facing habitats (T. Knoot, unpublished data). This focused approach to oak regeneration may be unsuccessful for several reasons: (1) from a timber perspective, high quality *Q. alba* and *Q. rubra* are generally not found on south-facing slopes (Jacobs and Wray 1992) and (2) this plan would potentially place oak species in direct competition with a highly successful invader: *R. cathartica*.

## Implications for management

Attention toward sustaining our oak forests now and into the future is urgently needed on both public and private lands (Lorimer 2003). While field studies continue to offer new information to forest managers, practical applications are needed for research results to be implemented. The direct results of my research suggest that invasion by and competition from *R. cathartica* may be of substantial concern when managing oak stands dominated by *Q. macrocarpa*. *R. cathartica* seems to be less of a problem at present within *Q. alba*- or *Q. rubra*-dominated stands, though attention should be placed on controlling *R. cathartica* invasions from the edges of these stands.

Not based on my research, but rather the sum of my understanding of the oak management literature, a successful oak management regime includes the thinning of non-oak species from oak forest understories accompanied by regular prescribed fire (Franklin et al. 2003, Hutchinson et al. 2005, Jacobs and Wray 2002, Lorimer et al. 1994). This regime should not only help to restore oak as a dominant species, but it will also benefit other plants and animals that depend on oak forests and it will assist in invasive species control (Archibold et al. 1997, Hutchinson et al. 2005, Lorimer et al. 1994).

Within Whitewater WMA, a reduction of leased crop land would allow for oak forest restoration through natural colonization and direct seeding on flat ridgetops. This would reduce edge length and minimize competition from the invasive shrubs *R. cathartica* and *L. tartarica* and other species that currently compete with oak species along the agricultural edges. Increasing forest stand size might also allow for more efficient management of larger tracts of forest land not interrupted by agriculture. Removal of non-oak saplings and trees would also aid oak species recruitment from the seedling to the sapling size class by reducing

competition for light. By thinning out the forest understory, deer hunters might effectively harvest more deer and thereby reduce one source of predation on both acorns and young oak recruits.

### **Implications for future research**

In terms of future research on oak forests in the Driftless Area, I perceive a great need to establish long term studies of forest dynamics in relation to different management regimes. Such studies will need to consider current forest composition, invasive species abundance, edge effects, and the goals of various management techniques.

A regional approach to understanding the distribution of invasive species in oak forest stands in the Midwest Driftless Area might begin by combining my data with remotely sensed data and/or forest inventories to build a predictive model of the potential locations of *R. cathartica* infestations. If the predictive capacity of such a model were high, it could provide a landscape and/or forest stand level method for identifying *R. cathartica* infestations and it could help to establish priority rankings for the implementation of control measures. Furthermore, there is a need to identify the full economic and ecological costs of alternatively controlling or not controlling *R. cathartica* infestations and other invasive plant species in the Driftless Area.

Studies assessing the impact of restoring bluff tops, which are predominantly in agricultural land use at present, to native vegetation would be helpful in understanding the full impact of agricultural edges and the potential for oak forest regeneration on the bluffs. Reducing the amount of agricultural edge habitat may be beneficial in simultaneously

reducing suitable habitat for *R. cathartica* establishment and in providing new habitat for oak recruitment (Archibold et al. 1997).

## LITERATURE CITED

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APPENDIX A. LIST OF ALL SPECIES FOUND WITHIN STUDY  
SITES. Taxonomy based on the USDA PLANTS Database (<http://plants.usda.gov>  
<accessed February 21, 2007>).

Scientific name	Common name
<i>Acer negundo</i> L.	Boxelder
<i>Acer saccharum</i> Marsh.	Sugar Maple
<i>Amelanchier arborea</i> (Michx. F.) Fern.	Downy Serviceberry, Juneberry
<i>Betula papyrifera</i> Marsh.	Paper Birch
<i>Carpinus caroliniana</i> Walt.	American Hornbeam, Musclemwood
<i>Carya cordiformis</i> (Wangenh.) K. Koch	Bitternut Hickory
<i>Carya ovata</i> (P. Mill.) K. Koch	Shagbark Hickory
<i>Celtis occidentalis</i> L.	Northern Hackberry
<i>Cornus</i> spp	Dogwoods
<i>Corylus americana</i> Walt.	American Hazelnut
<i>Crataegus</i> spp	Hawthorn
<i>Fraxinus americana</i> L.	White Ash
<i>Fraxinus nigra</i> Marsh.	Black Ash
<i>Fraxinus pennsylvanica</i> Marsh.	Green Ash
<i>Gleditsia triacanthos</i> L.	Honeylocust
<i>Juglans nigra</i> L.	Black Walnut
<i>Juniperus virginiana</i> L.	Eastern Redcedar
<i>Lonicera tartarica</i> L.	Tartarian Honeysuckle
<i>Malus</i> spp	Common Apple
<i>Ostrya virginiana</i> (P. Mill.) K. Koch	Ironwood, Hop Hornbeam
<i>Pinus resinosa</i> Ait.	Red Pine
<i>Populus deltoides</i> Bartr. ex Marsh.	Eastern Cottonwood
<i>Populus grandidentata</i> Michx.	Bigtooth Aspen
<i>Populus tremuloides</i> Michx.	Quaking Aspen
<i>Prunus americana</i> Marsh.	American Plum
<i>Prunus pensylvanica</i> L. f.	Pin, Fire Cherry
<i>Prunus serotina</i> Ehrh.	Black Cherry
<i>Prunus virginiana</i> L.	Chokecherry
<i>Quercus alba</i> L.	White Oak
<i>Quercus ellipsoidalis</i> E.J. Hill	Hill's / Northern Pin Oak
<i>Quercus macrocarpa</i> Michx.	Bur Oak
<i>Quercus palustris</i> Muenchh.	Pin Oak
<i>Quercus rubra</i> L.	Red Oak

## APPENDIX A CONTINUED.

Scientific name	Common name
<i>Quercus velutina</i> Lam.	Black Oak
<i>Rhamnus cathartica</i> L.	Common Buckthorn
<i>Rhus glabra</i> L.	Smooth Sumac
<i>Rhus typhina</i> L.	Staghorn Sumac
<i>Ribes</i> spp	Gooseberry
<i>Robinia pseudoacacia</i> L.	Black Locust
<i>Rubus idaeus</i> L. ssp <i>strigosus</i> (Michx.) Focke	American Red Raspberry
<i>Rubus occidentalis</i> L.	Black Raspberry
<i>Sambucus nigra</i> L. ssp <i>canadensis</i> (L.) R. Bolli	Common Elder, American Elder
<i>Staphylea trifolia</i> L.	Bladdernut
<i>Tilia americana</i> L.	American Basswood
<i>Ulmus americana</i> L.	American Elm
<i>Viburnum lentago</i> L.	Nannyberry
<i>Zanthoxylum americanum</i> P. Mill.	Pricklyash

**APPENDIX B. VEGETATION METRICS USED IN THE NON-METRIC  
MULTIDIMENSIONAL SCALING ANALYSIS (NMDS) OF THE PLANT  
COMMUNITY.**

Site	Mean tree importance values <sup>1</sup>					Saplings (saplings/ha) <sup>1</sup>								Shrubs (shrubs/ha) <sup>1</sup>					
	qual	quma	quru	tiam	ulam	acne	acsa	ceoc	osvi	prse	rhca	tiam	ulam	corn	prvi	rhca	ribe	ulam	zaam
1	7.6	0.8	35.0	8.0	12.1	44	50	6	39	61	0	44	89	2583	0	0	6417	167	83
2	0.0	15.3	15.6	3.6	17.6	17	0	22	0	128	178	17	61	0	1917	15583	6667	83	2167
3	11.4	1.5	18.6	11.9	25.9	106	0	28	0	56	83	94	233	0	250	1167	9833	417	667
4	1.8	5.2	39.9	3.3	15.0	11	0	17	117	17	0	22	150	333	1667	167	6333	1083	0
5	3.5	7.0	62.2	7.3	10.3	83	0	28	0	39	0	261	144	500	1667	83	3250	0	0
6	8.4	10.8	45.8	6.1	14.0	33	0	11	144	6	0	200	106	583	1000	0	1333	2250	667
7	15.0	0.0	35.7	4.5	32.3	83	6	44	17	33	0	56	194	83	333	0	4417	750	0
8	5.2	2.1	37.6	1.0	0.0	22	67	0	133	6	0	67	156	417	1000	0	2250	333	750
9	0.0	60.1	7.4	0.0	8.7	0	0	61	0	111	256	0	39	2417	167	1500	9083	83	833
10	15.0	0.0	51.2	0.0	0.7	0	372	0	89	0	0	0	0	0	917	0	1167	1000	0
11	0.0	30.4	30.7	0.8	15.8	11	0	22	0	44	44	11	78	1250	500	333	8000	250	1667
12	0.8	26.1	24.9	1.5	22.0	28	0	39	0	67	0	11	44	1667	250	83	11000	1000	917
13	0.0	7.9	11.7	3.7	48.8	50	0	106	0	22	44	67	206	1167	667	1333	9083	1000	0
14	0.0	21.2	22.8	29.2	21.4	61	0	22	0	28	39	150	189	167	833	1750	11583	583	0
15	16.5	4.4	40.0	5.3	9.0	17	0	11	278	0	0	28	111	917	1583	83	8917	2667	0
16	0.0	17.5	28.7	9.6	14.1	6	0	89	106	6	6	56	83	583	1750	750	8583	1583	1417
17	0.0	41.2	10.6	10.4	9.9	6	6	0	0	33	94	67	61	3083	417	5167	1000	583	3667

<sup>1</sup> qual = *Quercus alba*, quma = *Q. macrocarpa*, quru = *Q. rubra*, tiam = *Tilia americana*, ulam = *Ulmus americana*, acne = *Acer negundo*, acsa = *A. saccharum*, coec = *Celtis occidentalis*, osvi = *Ostrya virginiana*, prse = *Prunus serotina*, rhca = *Rhamnus cathartica*, corn = *Cornus* spp., prvi = *P. virginiana*, ribe = *Ribes* spp., and zaam = *Zanthoxylum americanum*

APPENDIX C. MIXED LINEAR MODEL PROGRAM CODE IN SAS (SAS INSTITUTE INC. 1999) TO TEST FOR DIFFERENCES IN ENVIRONMENTAL AND VEGETATION VARIABLES BY DISTANCE FROM EDGE: (A) MODEL ACCOUNTING FOR BOTH DISTANCE FROM EDGE AND SLOPE AND (B) MODEL ACCOUNTING DISTANCE FROM EDGE ONLY.

(a) Model accounting for distance from edge and slope.

```
Proc mixed;  
  Class plotid siteid transectid;  
  Model rs=plotid sl/s;  
  Random siteid;  
  Repeated /type=ar(1) subject=transectid;  
Run;
```

(b) Model accounting for distance from edge.

```
Proc mixed;  
  Class plotid siteid transectid;  
  Model rs=plotid /s;  
  Random siteid;  
  Repeated /type=ar(1) subject=transectid;  
Run;
```

## APPENDIX D. NMDS CODE USED TO PRODUCE TREE NMDS USING STATISTICAL PROGRAM R VERSION 2.3.1.

```
library(vegan)
library(MASS)
Alltrees <- read.csv('C:/Documents and Settings/Erik/My Documents/Research/Field
data/Graphs/R files/CSV 7 17/Alltrees.csv', as.is=T)
dim(Alltrees)
names(Alltrees)
Alltrees.data <- Alltrees[,c(-1)]
Alltrees.m <- as.matrix(Alltrees.data,)
Alltrees.dist <- vegdist(Alltrees.m, method='bray')
start <- initMDS(Alltrees.dist)
Alltrees.mds <- isoMDS(Alltrees.dist, start)
plot(Alltrees.mds$points)
Alltrees.mds2 <- metaMDS(Alltrees.m,distance='bray',autotransform=F)
plot(Alltrees.mds2)
plot(Alltrees.mds2,type='t')
Alltrees.mds2$points
plot(Alltrees.mds2,display='species',type='t')
Alltrees.mds$points
Alltrees.mds2$species
scores(Alltrees.mds2,type='t')
env <-read.csv('C:/Documents and Settings/Erik/My Documents/Research/Field
data/Graphs/R files/CSV 7 17/env.csv', as.is=T)
names(env)
env.data <- env[,c(-1)]
env.m <- as.matrix(env.data,)
Alltrees.fit <- envfit(Alltrees.mds2, env.m, permu=1000)
Alltrees.fit
plot(Alltrees.fit)
plot(Alltrees.fit, p.max=0.05)
plot(Alltrees.mds2,type='t')
plot(Alltrees.mds2,display='species',type='t')
plot(Alltrees.fit, p.max=0.05)
```

APPENDIX E. NMDS CODE USED TO PRODUCE  
VEGETATION NMDS USING STATISTICAL PROGRAM R  
VERSION 2.3.1.

```
library(vegan)
library(MASS)
Vegdata823 <- read.csv('C:/Documents and Settings/Erik/My Documents/Research/Field
data/Graphs/R files/CSV 7 17/Vegdata823.csv', as.is=T)
dim(Vegdata823)
names(Vegdata823)
Vegdata823.data <- Vegdata823[,c(-1)]
Vegdata823.m <- as.matrix(Vegdata823.data,)
Vegdata823.dist <- vegdist(Vegdata823.m, method='bray')
start <- initMDS(Vegdata823.dist)
Vegdata823.mds <- isoMDS(Vegdata823.dist, start)
plot(Vegdata823.mds$points)
Vegdata823.mds2 <- metaMDS(Vegdata823.m,distance='bray',autotransform=F)
plot(Vegdata823.mds2)
plot(Vegdata823.mds2,display='species',type='t')
Vegdata823.mds$points
Vegdata823.mds2$species
scores(Vegdata823.mds2,type='t')
env <-read.csv('C:/Documents and Settings/Erik/My Documents/Research/Field
data/Graphs/R files/CSV 7 17/env.csv', as.is=T)
names(env)
env.data <- env[,c(-1)]
env.m <- as.matrix(env.data,)
Vegdata823.fit <- envfit(Vegdata823.mds2, env.m, permu=1000)
Vegdata823.fit
plot(Vegdata823.fit)
plot(Vegdata823.fit, p.max=0.05)
plot(Vegdata823.mds2,type='t')
plot(Vegdata823.mds2,display='species',type='t')
plot(Vegdata823.fit, p.max=0.05)
```