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DEER AND SEDGE EFFECTS ON TREE SEEDLING DYNAMICS IN NORTHERN TEMPERATE FORESTS

By

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ABSTRACT

DEER AND SEDGE EFFECTS ON TREE SEEDLING DYNAMICS IN NORTHERN TEMPERATE FORESTS

By

Jesse Allen Randall

Since the mid-20th century, a combination of forest and wildlife management practices in northern Michigan have to led to white-tailed deer (*Odocoileus virginianus*) populations that are perhaps unprecedented historically and approximately four-fold higher than pre-European settlement estimates. Selective browsing of vegetation by deer at high densities may alter vegetation composition and structure, and impact ecological and economic values including forest tree regeneration. In addition to the proximal effects of browsing, deer- altered vegetation communities, have been hypothesized to persist if deer are reduced, by competitively excluding the reinvasion of deer sensitive species. For aspen and sugar maple dominated systems, I used a series of natural and manipulative experiments to 1) quantify the impact of deer browsing on forest understory composition and structure 2) compare the relative contribution of deer browsing and competition from deer impacted vegetation on tree seedling and forb dynamics, 3) investigate possible physiological mechanisms underlying competition between tree seedlings and deer altered vegetation, and 4) investigate techniques that could be used to decrease tree seedling competition with deer impacted vegetation. In 61 *Populus spp.* stands distributed among two relative deer density classes (~11 deer / km^2 and 6.8deer / km^2 deer densities), and a range of site productivities (Site index 12-25m @ 50years) and stand ages (12-44 years) deer strongly affected understory vegetation composition and

structure. Changes caused by higher deer density include greater fern and sedge mass, and, especially in more productive environments, decreased species diversity & richness Deer also reduced tree stem density and species richness (0.6m -4m tall) suggesting longer-term consequences for forest succession..

In managed northern hardwood forest with high long-term deer density (31/km2) removal of the *Carex pensylvanica* dominated understory vegetation had modest positive effects on tree seedling growth and survival and the magnitude of these effects increased with canopy openness (i.e. higher light levels). However, these effects, for larger tree seedlings were only apparent if deer were removed. These results indicate that deer effects on tree seedling dynamics supersede vegetation competition effects.

In the field, *Carex*-dominated understory vegetation lowered soil moisture availability to tree seedlings, potentially explaining lower growth and survival in the presence of vegetation. In a potted plant experiment with *Acer saccharum*, and *Carex pensylvanica* monocultures and mixtures, drought treatments reduced *Acer* seedling but not *Carex* survival. Surviving seedlings had shorter overall root and stems lengths following drought, while sedge root length or mass were not reduced by drought.

In one acre field plots, herbicide application in late autumn greatly reduced *Carex* density with little effect on other vegetation. However, given the dominant effects of deer on vegetation, only in areas with reduced deer could a seasonally timed herbicide application be effective in promoting tree seedlings.

Dedicated

To my wife Natalie & my entire family

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INTRODUCTION

General Overview

I begin this dissertation with a general introductory overview highlighting past forest and wildlife management practices that have resulted in an overpopulated white-tailed deer herd in parts of Michigan. I present a review of the direct and indirect effects of an overabundant deer herd on forested ecosystems from a global to an upper Midwest perspective. I go on to discuss the current state of knowledge surrounding restoration/remediation treatments used in forests to control competing vegetation, and discuss the need for new management techniques to selectively control vegetation in the understory of northern hardwood forests. Finally, I present the major questions addressed in each research chapter (1-4).

History of forest management and deer in Michigan

Historically, Michigan's forest communities were shaped by disturbance regimes (Palik and Pregitzer 1991) with return intervals varying over several orders of magnitude (Frelich 2002, Cleland et al., 2004). Prior to European settlement, Native Americans exerted direct and indirect pressure on Michigan's forested landscape through their use of fire and hunting. The combination of having forests that were much more contiguous, predator populations that were large and self-sustaining (cougars, wolves), and subsistence hunting kept deer numbers low over much of the Upper Midwest (2 - 4 deer/km^2 - Blouch 1984 and McCabe and McCabe 1984). Westward expansion helped bring about the era of big timber and fire (1800's to early 1900's), which cleared almost 92 % of Michigan's forestlands (Dickmann and Leefers 2003) and helped to drive deer numbers even lower as suitable habitat declined and market hunting increased.

Efforts to suppress wildfire allowed for early seral species (aspen) to regenerate, while those sites that did not burn regularly (northern hardwood, lowland conifers) flourished due to increased light reaching the understory and nutrient enrichment from decaying waste from past timber harvests. As forests were beginning to regrow, new laws which restricted deer harvests led to an overall increase in herd size until the 1950's. By the 1950's, the maturing second growth forest no longer provided favorable habitat conditions and deer numbers declined. Even though a second round of timber harvesting began in the mid-late 1950's, deer numbers did not respond until mosaic-like conditions (agricultural fields and forests at various successional stages), representing increased levels of edge habitat, were extensively developed throughout the northern portion of the state. As the deer population began to increase again (early to mid 1970's), land managers began to notice changes in forest understory compositions (increase in sedge) and seedling regeneration levels (decreases in desired species and increases in undesirables). By the late 1980's and into the early 1990's the deer herd approached two million animals in the state, and in certain core deer areas (those areas with extreme concentrations of deer- e.g. deer over-wintering yards) tree regeneration was no longer assured. (Mike Young, personal communication of International Paper's land management records, Michigan DNR).

Today the deer herd is estimated at roughly 1.8 million animals, well above the MDNR's stated herd size goal of 1.3 million animals (MDNR). Because deer management in Michigan is such a controversial topic, resource managers are often at odds with multiple stakeholders (hunters, loggers, farmers, conservation groups, auto insurance groups, etc.) as to how the herd should be managed. Resource managers must often defend their decisions concerning deer and forest management using studies that highlight deer impacts as justification for decreasing herd sizes or altering harvesting regimes.

The impacts of elevated ungulate populations

Deer impacts in forested systems are not just a Michigan phenomenon. Research work worldwide has quantified ungulate impacts on vegetation composition and structure (McNaughton 1985, Alverson et al., 1988, Pastor and Naiman 1992, Rooney and Dress 1997, Kielland and Bryant 1998, Hester et al., 2000, Crete et al., 2001, Russell et al., 2001, Motta 1995, Trembley et al. 2005, Weisberg et al., 2005, Danell et al., 2006). Although deer can affect certain vegetation which are particularly sensitive to deer browsing (e.g. hemlock seedlings) at low deer densities (Alverson et al., 1988), their impacts are greater in areas with high deer densities (Alverson and Waller 1997, Waller and Alverson 1997, Horsley et al., 2003, Côté et al., 2004, and Trembley et al., 2006), and in systems with greater site productivity characteristics (Milchunas and Lauenroth 1993, Hester et al., 2000).

When compared to unselective disturbance agents such as wildfire, landslides, windthrows, and ice storms, large scale herbivory may be a unique form of disturbance (Hulme 1996). Ungulates (e.g. deer, elk, moose) are highly selective towards the plants they consume, often causing understory forb layers to shifts away from being compositionally diverse (Marquis 1974 & 1981, Anderson et al., 2001), especially in areas with overabundant ungulate populations (Cornett et al. 2000, Crawley 1990, Coughenour 1991, McInnes et al., 1992, and Jefferies et al., 1994, VanDeelan et al., 1996, DeCalesta 1997, Horsley et al., 2003, Danell et al., 2006). Deer impacts on vegetation are difficult to generalize however because, 1) browsing affects several different vegetation characteristics and each of these may vary uniquely with browsing pressure, 2) for each of these characteristics, density interacts with other factors including, among others, characteristics of the plant community and resource availability (Weisberg et al. 2005, Wisdom et al. 2006) and 3) there are both temporal and spatial elements of deer browsing that can affect responses (Hester et al 2004, Danell et al., 1994). Horsley et al's, (2003) and Trembley et al's, (2006) work in productive maple-cherry forests in Pennsylvania and boreal balsam fir-birch forest of northeastern Canada, respectively, provide the best quantitative data to date concerning intermediate levels of deer browsing pressure for systems in the northeastern United States, but concrete threshold values to explain deer damage still eludes researchers (Horsley et al., 2003).

Overpopulated ungulates can have direct and indirect impacts on entire systems and their processes (Rooney and Waller 2003). Through browsing, the direct loss of overall plant biomass (Manseau et al., 1996) and tree form (multi-stemmed shrub form vs. a single stem – Gill 1992) in areas with high ungulate densities can have long term impacts to forest management (decreased timber quantity and quality resulting in decreased economic returns and overall forest sustainability) and system functioning due to changes in resource availabilities. Furthermore, as forbs never grow beyond the reach of deer, they are under constant browsing pressure, with sensitive species (indicators-Balgooyen and Waller 1995, and Rooney 1997 & 2000) being the first to be replaced with more browse tolerant /non-browsed species. Indirectly, deer, via shifts in vegetation compositions, can create a cascading effect on entire ecosystem and its functioning, which can persist under certain conditions, even if deer are removed (Stromayer and

Warren 1997, Augustine et al., 1998, de la Cretaz and Kelty 1999, George and Bazzaz 1999). Specifically, ungulate induced vegetation shifts can lead to decreased nutrient cycling rates when higher densities of low palatability, low nitrogen, decomposition resistant species dominate (Pastor et al. 1993, Pastor and Cohen 1997). This alone can change species compositions as species realign to reflect the change in nutrient availability. Compositional shifts can also increase plant competition levels as understories become saturated with the non-browsed or browse resilient species such as grasses, ferns, and sedges. These compositional shifts can also create feedback mechanisms as increased levels of plant growth (overcompensation) (McNaughton 1983, Belsky 1986) can lead to increased secondary ungulate browsing further altering composition. Overall, declines in forest productivity and ecosystem fertility (Risenhoover and Maass 1987) can be caused directly and/or indirectly by deer via deer induced shifts in composition. With declines in productivity and shifts in composition and forest structure, habitat quality for some forest birds (Hall and Root 1999), insects, amphibians, and small mammals (Hodorff et al., 1988) may decline. Eventually, long lasting, extensive shifts in vegetation compositions can alter the carrying capacity of the habitat, resulting in a reduction of ungulate health and declines in herd size (Davison and Doster 1997). To date, the indirect effects of overpopulated deer herds are not well understood and mainly exist as untested hypotheses because of the complex interactions between the temporal and spatial factors affecting deer browsing and a systems succession induced changes in form and processes.

Restoring deer influenced degraded forests

Reversing compositional and structural shifts through direct remediation activities is increasingly common, as more and more forested lands are being negatively impacted by elevated ungulate populations and increased populations of ungulate induced plant competitors. The most comprehensive work to date targeting the reduction of plant competitors has taken place in conifer systems (Cogliastro et al., 1990, Lautenschlager 1995, Bell et al., 1997, Vreeland et al., 1998, and Wagner et al., 2004). In these systems, emphasis is normally placed on increasing young seedling survivorship during the establishment phase to maximize potential crop tree production and not the overall ecological integrity and processes that maintain systems (Wagner et al., 2004). Applicable work in northern hardwood stands is much more scarce, as most treatments (i.e. herbicides, mowing, controlled burning) that control hardwood competitors (i.e. grasses, sedges, and ferns) also impact the northern hardwood crop trees. Working to promote northern hardwoods in areas with high deer densities by controlling competing vegetation, has to date, resulted in a better understanding of deer impacts and the effectiveness of various herbicides to control competing vegetation (Horsley 1981, & 1990), but no concrete evidence has been forthcoming that treatments can be used to overwhelm and thus overcome overabundant deer herd browsing. The use of strategically timed vegetation manipulation treatments which do not interfere with previously established northern hardwood crop trees and which, at the very least, maintains herbaceous layer diversity have been tried only sparingly (but see Horsley 1981, Willoughby 2006)

Deer effects have been studied by several researchers in various northern temperate forests (Aspen – Campa 1989 & Raymer 1996, Cedar - VanDeelan et al., 1996 & VanDeelan 1999, Hemlock – Frelich and Lorimer 1985, Mladenoff and Stearns 1993, Northern hardwoods – Buckley et al. 1998, Rooney and Waller 2003), often times with an emphasis on individual components (understory composition, overstory structure, deer available forage quality and quantity) at a specific site or time since disturbance (but see Raymer 2000). In Michigan, it is now of greater importance to managers and practitioners for researchers to identify if linkages exist between ungulate browsing and other potential successional drivers in forested systems. A recently conducted survey spanning all major forest types in Michigan revealed that large shifts in structure and composition were evident in high deer areas, but as important, high sedge densities often accompanied elevated deer densities (Randall and Walters unpublished data). In these areas, the declines in forb and seedling composition and structural complexity cannot be ascribed solely to increased deer browsing as high sedge or fern cover, resulting from preferential deer herbivory may directly impact seedling dynamics via competition. Furthermore, sedge could increase due to factors other than the direct or indirect effects of deer browsing. For example, a long history of selection harvesting may favor sedge, as relatively high light levels are maintained for vegetation near the forest floor (Metzger and Schultz 1984, Horsley 1990, Wiegmann and Waller 2006) but see Jenkins and Parker 1999). In addition, populations of invasive earthworms have even been found to cause declines in forb and seedling communities (Hale et al., 2006, Frelich et al., 2006), and increased levels of sedge cover compared to areas without worms.

As forest composition and structure can be affected by several variables other than deer, accounting for those variables (e.g. site and stand variation - Pinno et al., 2001) while attempting to understand the mechanisms at play between deer, sedge, and deer X sedge should enable managers to make better resource based decisions in the deer and sedge dominated systems. This increase in knowledge surrounding the mechanisms and the direct and indirect effects of deer should improve not only forest health and sustainability, but also the health and sustainability of the deer herd.

The overarching goal of this dissertation was to use natural and manipulative field based studies, along with a controlled environment study, to tease apart potential drivers of the regeneration failure currently ascribed almost exclusively to overabundant deer. In addition to providing resource managers with a better understanding of the sedge/deer system, I also hoped to find restoration treatments that could be used to control sedge in a manner that would not harm existing seedling and forb populations.

Specifically, in the field portion of the dissertation (Chapters 1-3), I asked:

1) i). How does deer density affect the cover, mass, species richness, diversity, nitrogen content and structure of forest understory herbaceous and woody vegetation?
   ii) Do site index and/or stand age have interacting effects with deer on vegetation characteristics?
   iii) What are the potential successional legacies of changes in tree sapling composition and densities, and what are their management implications?
2. i) What are the relative impacts of main effects and interactions of deer and of a

sedge-dominated understory on tree seedling establishment, survival and growth, and forb diversity in highly productive northern hardwood stands dominated by sugar maple?

ii) If there are effects of deer and sedge on seedling growth in these productive stands, can this be associated with changes in soil nitrogen and water availability?

iii) If there are effects of sedge on growth and survival, how do these effects vary with light availability?

3. i) If high sedge cover is partially responsible for inhibiting the reestablishment of tree seedlings and forbs, is it possible to reduce sedge covers with management interventions (timed herbicide applications) such that tree, shrub, and forb establishment would increase?

   ii) What are the effects of increased canopy openness conditions on seedling and forb establishment and survival, and do responses change based on vegetation manipulation treatment?

4. Under controlled environment conditions, I asked:

   i) Can *Carex* draw soil water to lower levels than *Acer saccharum* seedlings?

   ii) Does *Carex* have greater survivorship than *A. saccharum* seedlings at low water availability?

   iii) Does a drought event negatively affect *A. saccharum* growth?

   iv) Does *Carex* negatively affect soil mineral nitrogen availability?

This dissertation represents a compilation of publication manuscripts developed from work which took place in aspen dominated stands (chapter 1), productive northern hardwood sugar maple stands (chapters 2&3), and under controlled environmental conditions targeting sedge-maple interactions during and after drought (chapter 4). The common linkage throughout this dissertation is elevated levels of plant competitors (sedge) and/or the effects of overabundant white-tailed deer on vegetation dynamics. Results along these lines further both basic and applied knowledge in forest systems with overpopulated deer herds and an almost uniform cover of sedge in the understory. Briefly:

In Chapter 1, to observe vegetation dynamics and address questions 1i-iii from above, I designed an experiment that accounted for stand age (12-44 years) and site productivity (~12-25 m @ 50 years) influences in each of two long-term deer densities categories (11 vs. 6.8 deer/km^2). Aspen monocultures were used to minimize the influence of overstory compositions on resources levels in the understory.

Research work which formed the basis for chapter two (questions 2i-iii) was driven by the desire to specifically address the influence of both sedge and deer individually and in combination with each other on understory vegetation composition and structure, as well as system functioning from a belowground resource availability standpoint. To do this, a series of deer exclosures and vegetation removal treatments manipulated deer and understory vegetation in sugar maple dominated forests.

In response to the work and results from chapter 2, and driven by conversations with forest managers at local, state, federal, and industrial levels it became evident that silvicultural techniques utilizing cost effective herbicide treatments beneath selectively harvested overstories which control increased populations of sedge, while at the same time minimized the impacts to established hardwood seedlings and understory forbs, were lacking. I addressed questions 3i-ii using seasonally timed spray treatments, 0.2 ha in size, under the canopy of selectively harvested sugar maple forests. In addition to direct tests of treatments, levels of harvesting intensity varied throughout the stand and provided a gradient of canopy openness conditions to test the response variables against.

Finally, chapter four is a mechanisms paper. This manuscript presents results quantifying the impact of drought on sedge and sugar maple seedling survival and growth. It furthers the understanding of sedge/maple interactions witnessed in the field-based portions of the dissertation.

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CHAPTER 1

DEER DENSITY EFFECTS ON VEGETATION IN ASPEN FOREST UNDERSTORIES OVER SITE PRODUCTIVITY AND STAND AGE GRADIENTS

Executive summary

I quantified main effects and interactions of deer density, site productivity (site index), and stand age on forest understory vegetation structure and composition characteristics in the understory of closed canopy aspen stands in Michigan's lower peninsula. Sites on state-owned lands (6.8deer km^{-2}) and on a nearby private hunt club (~11 deer km^{-2}) comprised two long-term (>30 years) deer density categories. Deer density, stand age and site index affected several vegetation characteristics, but interactions were generally weak and deer effects dominated. Higher deer densities resulted in approximately 3-fold greater bracken fern (415 kg/ha vs. 130 kg/ha) and sedge biomass (220 kg/ha vs. 84 kg/ha), 90% lower herb biomass (1.1 kg/ha vs. 10.2 kg/ha), 3.4-fold greater woody stem (<0.25m tall) biomass (9.3 kg/ha vs. 2.7 kg/ha), and 90% lower woody stem densities (0.6m – 4m tall) with only *Prunus virginiana* saplings at high deer density. Aspen stand age and deer interacted strongly on sedge biomass with high deer densities areas having much greater sedge in young than old aspen stands, while in lower deer density areas sedge was found at low densities across all ages. Both fern and sedge mass were high at high deer and high SI, but near zero at lower deer. Bracken fern is typically abundant on poorer sites suggesting that higher deer may be driving vegetation on richer sites toward species that are both less palatable and adapted

to poorer sites. Herb layer species richness and diversity were greater at lower than higher deer density. Deer density did not affect vegetation N concentrations, but total vegetation N content in the deer browse zone (i.e. < 1.5 m height) was higher (11 vs. 3.6 kg N /ha) in high deer density areas due to higher sedge and fern biomass. In summary, controlling for overstory density and composition with closed canopy aspen stands, I found that higher long-term deer densities had strong impacts on understory vegetation, with changes in sapling composition and density potentially affecting successional trajectories on long time frames. Relative effects on understory vegetation were generally greater on more than less fertile sites, which is consistent with data for non-forested systems.

Introduction

Interacting with a myriad of factors, ungulate browsing is a key driver of vegetation dynamics in ecosystems worldwide (Russell et al. 2001, Pastor and Naiman 1992, Alverson et al., 1988, Hester et al., 2000, Crete et al., 2001, Trembley et al., 2005, Weisberg et al., 2005, Danell et al., 2006). In the forested ecosystems of Eastern North America, white tailed deer (*Odocoileus virginianus,* hereafter called deer) are often the dominant ungulate herbivore. In the last several decades, land use practices and wildlife management policies have resulted in deer densities that are thought to be historically unprecedented in much of its range. There has been widespread concern that deer are having strong impacts on forest vegetation composition and structure, and research to date has demonstrated some of these effects (e.g. Rooney and Waller, Augustine, Horsley, Tremblay). Deer impacts on vegetation are difficult to generalize however because, 1) browsing affects several different vegetation characteristics and each of these may vary uniquely with browsing pressure, 2) for each of these characteristics, density interacts with other factors including, among others, characteristics of the plant community and resource availability (Weisberg et al., 2005, Wisdom et al., 2006) and 3) there are both temporal and spatial elements of deer browsing that can affect responses (Danell et al., 1994, and Hester et al., 2004).

Examples of vegetation characteristics affected by deer in Eastern North America include reduction or local extirpation of highly browse sensitive species (*Taxus brevifolia*, Parks et al., 1998, *Maianthemum canadense,* Balgooyen and Waller 1995, Rooney 1997, *Tsuga canadensis and Thuja occidentalis* Rooney and Waller 2003), decreased density of reproductive structures on browsed plants (*Trillium spp.*, Anderson

1994; total forest floor community Tremblay et al., 2006), composition changes and decreased diversity of tree regeneration (Horsley et al., 2003, Tremblay et al., 2006), and increases in non-preferred browse species (e.g. ferns, Horsley et al., 2003). The magnitude of deer effects may vary uniquely among response characteristics. For example highly sensitive species, like *Tsuga canadensis* saplings growing the in zone of deer herbivory (i.e. to approximately 1.5 m height) can be locally extirpated at deer densities as low as $4/km^2$ (Alverson and Waller 1997), whereas density of black cherry (*Prunus virginiana),* a non preferred browse species, does not increase in density in harvest gaps until deer density exceeds $15\ km^2$ (Horsley et al., 2003).

Obviously, vegetation dynamics depends on factor other than deer herbivory, and these factors may interact with deer herbivory in complex ways. For example, the impacts of herbivory may vary among vegetation communities that differ in their evolutionary browse histories (Milchunas and Lauenroth 1993), or in their particular composition and the differences in competitive interactions and relative preferences to herbivores among species.

Resource availability could also influence plant responses to deer browse pressure. For example a metanalysis of ungulate grazing effects on non-forested systems indicates that richer sites (higher nutrient and/or water avaialability) are more negatively impacted than poorer sites (Milchunus and Lauenroth 1993), perhaps because plants on poor sites are more prone to disturbance and drought and thus allocate more biomass and energy storage to roots, thus making them more grazing tolerant. Responses should vary with light availability as higher light energy would enable plants to quickly compensate for tissue loss, and for tree saplings, allow individuals to outgrow deer's reach in height quicker (Weisberg et al., 2005). Differences in vegetation responses to deer herbivory between harvested and unharvested areas (e.g. Horsley et al., 2003, Tremblay et al., 2006) are a clear reflection of the interaction of resource availability and deer density affects on vegetation.

The forest understories of closed canopy forests may be especially sensitive to deer browse pressure. Because of strong light limitations to growth in forest understories, the consequences of a given amount of tissue removed for plant fitness as well as for community structure and composition is greater and more long lasting than in less growth limited environments. Furthermore, deer browse impacts on tree sapling in forest understories could change the tempo and composition of forest succession for decades to centuries because their browse could affect the composition and density of saplings that recruit to canopy positions.

I designed a study to test the effects of differences in long-term deer density and site quality on vegetation composition and structure in the understories of 61 closed canopy aspen stands distributed over state-owned and private hunt club land that have differed in deer density for more than 30 years (lower vs. higher respectively). I focused on the understories of closed canopy mono-dominant stands because 1) these criteria insured that light availability, a strong driver of vegetation dynamics, varied minimally among my study plots, and 2) because deer effects could strong due to light limitation and have long legacies. Locating stands across site quality gradients (assessed using site index, (Lundgren and Dolid 1970) allowed me to examine the notion that deer herbivory has greater impacts on more fertile/moist sites. In addition, I located stands among a fairly limited range of ages and used age as a variable, reasoning that understory vegetation characteristics could vary somewhat with age (Pinno et al., 2001, Leiffers et al., 1996) despite the fact that all sites were in young, fully stocked, self thinning stands. Given this design I was able to address the following questions:

2) How does deer density affect the cover, mass, species richness, diversity, nitrogen content and structure of forest understory herbaceous and woody vegetation?
3) Do site index or stand age have interacting effects with deer on vegetation characteristics?
4) What are the potential successional legacies of changes in tree sapling composition and densities, and what are their management implications?

Methods

Study Area

My study sites were in aspen (*Populus tremuloides* Michx. and *P. grandidentada*) stands located on state and private forestlands in Roscommon, Gladwin, and Clare counties MI, USA. The study region's long-term climate averages include: annual precipitation, 730 mm; growing season (May-August) precipitation, 300 mm; annual snow fall, 192 cm; growing season length (days where the minimum temp is > 0 °C), 126 days; and July mean temperature, 21 °C (NOAA National Virtual Data Systems). The region contains level to moderately undulating hills (0-18% slopes) with post-glacial geological features dominated by ice contact ridges and sandy outwash plains. Soils in the region are a mixture of Rubicon – Menominee, Graycalm and Grayling sands (USDA soil survey of Gladwin County 1972 and Roscommon County 1972).

Site Selection

In early summer 1999, I selected aspen-dominated sites in approximately equal numbers on two ownerships: a) within Mid Forest Lodge (MFL), a 7,317 ha private hunting club, characterized by high long-term deer densities; and b) on state lands, located >1.6 km and < 10 km from MFL and characterized by lower deer densities than MFL. Unlike state lands, MFL has hunter access restrictions, an aggressive winter-feeding / food plot program, and, in the past, club rules limiting doe harvests.

Several decades of track count data collected in a uniform manner each year by MFL indicated sustained high deer densities (unpublished MFL data), and although similar data do not exist for state lands, larger-scale regional deer pellet count data indicated much lower deer densities on these lands. To confirm these a priori classifications, I conducted deer fecal pellet count estimates (described below).

From a broad list of candidate stands, I selected 32 stands with relatively higher deer densities (i.e 11 deer/km^2, MFL property) and 29 with relatively lower deer densities (i.e. 6.8 deer/km^2, state property), distributed among two target aspen stand age strata (10-20 yr old and 30-40 yr old) and three relative site productivity strata (low, moderate, and high). MFL and DNR harvest records were used to identify potential aspen stands that fell within five years of the two age strata. Productivity strata were determined from landform mapping and interpretations of vegetation characteristics collected on site according to an ecological classification system (Cleland et al., 1993). Candidate sites were discarded if management records did not match site criteria (e.g. not aspen dominated), were not closed canopy, self-thinning stands, or if they came from over-represented strata. Within a selected stand I randomly located a sampling area, and randomly located a site plot center which I marked with a permanent metal stake.

Measurements

Deer density estimates

In early April, 2001, I counted deer fecal pellets just after snowmelt on a randomly selected subset of sites within each deer density class, (29 of the 61 sites). Starting at the permanent center stake, an observer walked four-150 m long transects along the cardinal directions (N,S,E,W) and counted pellet groups within 2 m of either side of the transect (2400 m^2 sample area). Spring deer population densities were estimated using the following formula modified from Hill (2000):

$$\boxed{\text{Deer}\cdot\text{km}^{-2} \quad \frac{\text{pellet groups/m}^2\text{ sample area} \times (10{,}000\text{ m}^2\cdot\text{km}^{-2})}{13.37\text{ (fecal groups}\cdot\text{deer}^{-1}\cdot\text{day}^{-1}) \times (\text{leaf off period in days})}}$$

Vegetation

A four-layer nested sampling plot design, centered over the permanent site center stake, was used to measure forest vegetation composition and vertical structure during the peak of the growing season (late July). Plot dimensions and the characteristics measured were as follows: 1) in a 3 x 3 m grid, % cover by species of all vascular plants <25 cm tall estimated occularly and simultaneously by two observers (to remove observer error, the same two observers conducted all % cover estimate measurements at all sites); 2) in a 3.1 m radius circular plot, heights of all woody tree and shrub stems 0.25 m to 1.4 m in height by species; 3) in a 5.64 m radius circular plot, the diameter (at DBH), total height (hypsometer pole) of all tree and shrub stems by species > 1.4 m tall and <10 cm DBH; and, 4) in a 12 m radius, the diameter at 1.4 m height and total height (Sunto® precision clinometer) of all trees > 10 cm DBH by species.

To characterize forest floor layer vegetation composition, biomass and nutrient content in July 2001, I established a 1.5 m^2 plot 15 m north of the permanent stake. In this plot, I described the forest floor vegetation as detailed above and then destructively harvested all aboveground biomass of the forest floor vegetation layer including shrub and tree seedlings <0.25m in height. Harvested vegetation was separated into 5 categories (forbs, sedge & grass, bracken fern, and shrub and tree seedling (hereafter referred to as woody seedling) leaves and stems) in the field. The sedge and grass category was dominated (> 90%) by *Carex pensylvanica* Lam. and will hereafter be called sedge. I dried the samples at 70 °C for 72 hours in the lab prior to measuring dry mass. All dried samples were passed through a Wiley mill, pulverized in a hammer mill (KLECO – Kinetic Laboratory Equipment Company, Visalia, CA) and a 7-10 mg subsample was analyzed for N concentration by the Dumas combustion method with a CHN analyzer (Carlo Erba, Milan, Italy). *Vaccinium* was excluded for analyses because of its absence in higher deer density areas and its overall small and inconsistent mass in lower deer density sites.

Site Productivity

To determine and index of site productivity, I measured age at 1.4 m height for two co-dominant trees at each site. To age trees I used either two increment cores at 90° angles from one another, or a single radial cross section taken after felling the tree. Air-dried cross-sections (n=78) and cores (n=mounted on grooved wooden boards were sanded with 220 grit sandpaper prior to counting and recording annual rings on scanned digital images with WinDendro (Reġent Instruments, Blain, Quebec). On trees which were increment cored (n =20), I measured tree heights using a Sunto® precision clinometer. Felled tree heights were determined with a tape measure. To check clinometer measurement accuracy I compared clinometer and direct height measurements for a subset of felled trees. I used age and height data to determine site index from published site index curves for the Lake States region (Lundgren and Dolid 1970).

Analysis

Preliminary analyses of stand age and site index data revealed that my a priori age and productivity target categories resulted in relatively continuous and even distributions of both stand age and site index over both deer density categories. Thus, I chose to consider these variables as continuous rather than categorical. Due to the fact that age and site index ranges differed somewhat between higher and lower deer density strata, I selected a subset of stands to achieve similar ranges for both stand age (12-24) and site index (17-26 m at 50yrs). This subset was used for some analyses (structure and tree species composition) with the objective of minimizing confounding deer density with SI and/or stand age. I used JMP (5.1) statistical software (SAS institute, Cary, NC, USA) for all statistical analyses.

Seedlings >0.25 m tall were placed into height classes to facilitate analyses of stem density and vertical structure. Vegetation was analyzed with mixed least squares models using a full factorial treatment design with main effects deer density (higher vs. lower), as a discrete, nominal variable, and site index and stand age as continuous variables. If model results indicated that interaction terms were insignificant beyond the threshold suggested for pooling variances ($P > 0.25$, Bancroft 1964), then the highest order interaction term with the highest P value was removed and the model was re-run.

This process was repeated iteratively until a final model was constructed where all interactions >0.25 were removed.

I examined species richness for vegetation <0.25 m tall by bootstrapping data using R statistical software to obtain multiple estimates of the number of unique species for each area (9 m^2 plot) gradation. The mean of these estimates were used to develop smoothed species area curves for each combination of deer density (lower, higher) and site index (low, high) categories. Initially, I separated stands into young and old stand age cohorts, but due to a non-uniform distribution of site productivities in older stands I chose to only evaluate young stands. The methodology for bootstrapping dictated that I assign productivity classes rather than using continuous data. Therefore I chose two classes that included sites at lower and higher ends of the SI range and excluded intermediate sites to clearly highlight differences.

Similar to the previously mentioned methods for analyzing forest structure and composition, I tested Shannon-Weiner diversity indices (H') on a subset of sites, which had uniform stand age (15-38) and site index (17-26 m at 50yrs) ranges across the two deer density strata.

Results

Deer density

Spring 2001 fecal pellet counts collected for a subset of sites showed that MFL had 62% greater relative deer density than adjacent state owned lands (11 vs. 6.8 deer/km^2, respectively). Large variation among sites made these differences only marginally significant (P=0.068). Corroborating my independent pellet counts, track count data collected by MFL members since 1968 indicate an average herd size of 10 deer/km^2 over the last 25 years prior to 2001. Additionally, MDNR deer pellet counts collected in 1981, 1995, and 1999 (averaged across the three sampling years) estimated 21 deer/km^2 in the MFL and 15.7 deer/km^2 on adjacent state lands. Although values differ among estimation methods and time frames they consistently indicate sustained long-term relative differences in deer populations between my higher and lower deer density strata. Vegetation browse indicators (Balgooyen and Waller 1995, Rooney 1997 & 2000) were also consistent with my higher and lower deer density catagories. *Mianthemum canadensis* cover was ~11-fold greater at higher deer than lower deer ($P<0.0001$), while *Gaultheria procumbens* and *Aralia nudicaulis* were 3.5-fold greater.

Vegetation biomass, structure, and composition

Several forest floor vegetation mass and structural characteristics varied with deer density, site index, stand age, and/or their interactions, but deer effects generally dominated (Appendix 1.1, 1.2). Total aboveground forest floor vegetation biomass (i.e. ferns, sedges/grasses, forbs, low shrubs, and woody seedlings <0.25 m tall) was greater in higher than lower deer density areas (657 vs. 252 kg/ha, $P< 0.0001$). Although bracken fern and sedge dominated forest floor biomass in higher and lower deer density categories, higher deer density sites had, on average, three times greater bracken fern, sedge, and woody plant mass, and one-tenth the forb mass (Figure 1.1). Bracken fern and sedge mass decreased as site productivity increased and mass was greater at higher-than lower deer density over the entire range of site index (Figure 1.2A & B). Total aboveground vegetation decreased with increasing site productivity but only in areas with high deer densities. Sedge mass decreased with increasing stand age such that sedge density was similar at high and low deer densities in stands >35 years old (Figure 1.2C).

In contrast, woody plant density <0.25 m in height increased with aspen stand age but did not interact with deer density (Appendix 1.1D, Figure 1.2D).

Higher deer density decreased forest floor layer plant species richness and the magnitude of the decrease was greatest at higher productivities (45 % decline in richer sites vs. 21 % decline in poorer sites vs. their respective lower deer density site productivity controls). (Figure 1.3, Appendix 1.2D, & 1.3). I found no interactions between deer density and stand age or site productivity levels for Shannon-Weiner diversity values (H'). H' increased with increasing site index for both deer densities and was uniformly lower (24%) in higher than lower deer areas across the range of SI (Figure 1.4). Stand age showed no relationship with diversity (Appendix 1.2D).

Deer density affected total shrub and tree density, but effects varied among height classes and with stand age and site quality (Appendix 1.2A-C). In low deer density areas, total stem density in all height strata generally increased with stand age and site index, but deer sharply reduced woody stem density in 0.6-1.5 m and 1.5 –4.0 m strata over the range of SI and stand age (Figure 1.5). For a data set restricted to a common range of SI and age, higher deer density had 84.4% lower total stem density than lower deer density (*P*=0.0003, Figure 1.1E), and only black cherry stems remained. For the 1.5 m to 3.9 m tall height class, a zone affected by past deer browsing, results were similar to the 0.6-1.5 m tall height class with higher deer resulting in 91% lower stem densities (*P*=0.0092, Figure 1.1F) with witch hazel, oaks and red maple nearly eliminated and mostly black cherry stems remaining (Figure 1.5, Appendix 1.4).

Vegetation nitrogen

Greater total N was found in forest floor vegetation at higher than lower deer density (Figure 1.6A.). This difference was not driven by higher tissue concentrations (Appendix 1.5C-G), but by greater total vegetation mass due to increased sedge, bracken fern, and woody seedling < 0.25 m tall (Figure 1.1A, B, & D). Tissue N concentrations for bracken fern, sedge, and forbs increased with SI and decreased for tree seedling leaf N and stem N concentrations with stand age (Appendix 1.5). In contrast to total forest floor vegetation N content, non-bracken and sedge (i.e. tree/shrub seedling leaf (< 0.25 m tall) + forb) N content was roughly twice as high in lower deer density areas (Figure 1.6B) and deer density, stand age, and site index model effects were of approximately equal magnitude (Appendix 1.5B). Forest floor seedling + forb N increased with site index and stand age (data not shown) and decreased with deer density (Figure 1.6B). The lack of interactions with deer density indicates that deer reduced N content similarly across stand ages and site indices (Appendix 1.5).

Discussion

All lines of evidence used in this study to assess the deer population status (site specific fecal pellet counts, historical track counts, and MDNR estimates) showed that my relative deer density categories across the two ownerships were in fact different. These differences in relative deer density levels strongly influenced aspen forest understory plant composition, mass, structure and N content, although some of these responses were dependent on site index and stand age. Deer affected forest floor vegetation in younger more than older stands (range 12-44 year old), where higher deer densities areas had much greater bracken fern and sedge mass than lower deer density areas. The strong stand age x deer interaction on sedge mass could possibly be explained by sustained low light availability beneath closed aspen canopies (Pinno et al., 2001). Over time, the low light availability beneath aspen stands may diminish shade intolerant sedge whose populations were initially elevated by the combination of high light following harvesting and lack of browsing by deer. In aspen stands with elevated ungulate densities, browsing did in fact cause canopies to be less dense and allowed for more "old field" higher light demanding forb species to establish and grow while more shade tolerant forbs were found in exclosures (Raymer 2000). Although all of my sites were closed-canopy aspen stands, higher sapling density in lower deer density areas may have intercepted more of the light transmitting through the aspen crowns further lowering light levels at the forest floor. I did not measure light directly, but young stands at low site index had few stems >0.6 m tall in either higher or lower deer density areas, and it was in these stands that some of the largest differences in sedge and fern density between higher and lower deer density occurred. Thus, I did not find indirect support for my speculation that differences in light between higher and lower deer density areas affected sedge and fern density.

The increase in bracken fern at higher site index suggests that less palatable vegetation common to lower fertility-more disturbance prone areas (Berger and Kotar 2003) may become more common in higher fertility areas when deer browse pressure is high. The reduced light associated with increased fern cover may have long-term implications for seedling establishment (George and Bazzaz 1999) as well as consequences to below-ground nutrient cycling (for vegetation induced shifts in belowground cycling see Pastor et al., 1993). Increases in non-browsed species (fern and sedge) may also alter disturbance regimes on richer more productive sites (more frequent surface fires etc) such that in forests that are not evolutionarily adapted to fire (northern hardwoods) we may see drastic changes in all vertical layers following a ground layer fire carried by bracken and sedge litter.

Changes in composition associated with high deer density might be partially explained by species characteristics. Bracken fern and sedge are both rhizomotous, clonally growing species, which lack permanent aboveground stems. Additionally sedge's intercalary meristems may reduce their sensitivity and susceptibility to deer browsing. Although I found no differences in N concentrations, an index of protein concentrations, between sedge, fern, woody seedling and forbs, sedge and fern may be less desirable as browse because of accumulated silica in foliage (Prychid et al., 2003). Thus, over time, as deer selectively remove more nutritionally desirable and non-rhizomous forb and tree species, fern and sedge, via clonal growth, are able to quickly sequester the growing space opened by browsing. Ultimately this may lead to their dominance, and in turn may be perpetuated by resource sequestration (e.g. light interception by bracken fern (de la Cretaz and Kelty 1999, George and Bazzaz 1999), nutrients (Knoop and Walker 1985), moisture (Dodd et al., 1998), and germination sites (Horsley 1993a & b)).

Forest floor vegetation N content was elevated in higher deer density areas, and these effects were due to increased amounts of vegetation (mostly sedge and bracken fern), and not by increases in tissue N concentrations. It is important to note, however, that forest floor vegetation samples did not include shrub and tree stems >0.25 m tall. Stem density was lower in the 0-0.6 m tall class but greater in the 0.6 - 1.5 class at lower deer densities. If mass 0.25 – 1.5 m had been included, absolute differences in total N between higher and lower deer densities would probably be diminished somewhat, but rank differences would likely be preserved because there is only one additional 0.6 - 1.5 m tall stem per 5 m^2. The increase in forest floor vegetation caused by deer should not be misinterpreted as an increase in available N to deer, as the increase occurs in sedge and fern.

Greater forest floor seedling biomass (0-25 cm, Fig 1D) and stem density in the 0-0.6 m tall class in higher deer density areas is a reflection of high browse pressure lowering the overall stature of shrubs and tree seedlings, and a snow pack which provides minimal browse protection to seedlings throughout the winter months. These older, stockier individuals, in shorter height classes, fail to grow into the higher classes and result in a drastically altered vertical structure. Although my study was not designed to test hypotheses concerning fern-tree seedling resource competition, bracken fern's potential impacts on seedling resources, including light, could be inhibiting seedlings from growing into taller height classes (George and Bazzaz 1999).

The near complete loss of seedlings in the1.5m – 4m height class indicates both the legacy of past deer densities and it portends a shift in tree species composition in the future, if the stands are not maintained for aspen by clearcutting. Based on my data, areas with high deer density will likely have black cherry and little else, as oak, red maple and witch hazel were essentially extirpated by deer. Others, (Tilgham 1989, Yahner 1995, Raymer 1996, and Horsley et al., 2003) have documented increasing stem densities of black cherry in higher ungulate areas along with red maple. It is possible that the red maple component, or lack there of, in the understory was no more than an artifact of past stand harvesting or cleaning practices, which could have promoted or reduced seed availability or sprout origin stems of these species.

As deer browse has favored dominance by sedge and fern, which are less palatable and/or inaccessible to deer for portions of the year, browsing pressure on the remaining palatable plants (i.e. woody seedlings and forbs) will most certainly increase. Bergvall et al., (2006) termed this "neighbor contrast susceptibility". This mechanism is proposed to hold true as long as deer are unselective as to the area that they browse while being highly selective as to what they browse. Therefore, any management regime that helps to maintain elevated deer densities in a fixed locality for extended periods of time (food plots, supplemental feeding, natural deer yarding areas, and agricultural/forest matrices) will promote the neighbor contrast susceptibility mechanism. Hunt clubs like MFL, that have maintained high deer densities for decades, are a prime example of the conditions promoting neighbor susceptibility, and as such, effects of deer on vegetation can be expected to be greatest here and in other areas with sustained high long term deer densities.

Given that deer in northern lower Michigan have home ranges that are often between ~220 ha (2.2 km^2) and 500ha (5 km^2)(Sitar 1996, and Garner 2001), and winter-summer migrations in the area can be as long as 10km (Garner 2001), the minimum buffer used in this study between higher deer density areas and lower deer density areas (1.6 km) was a potential source of error. Given the multiple lines of evidence used to determine if deer density categories were in fact different (explained above), I feel that overlapping use of the area by deer was minimal, the categorized deer densities differences significant, and that the observed deer effects on the system were real.

Altered composition and structural attributes caused by chronic browsing is not limited to the aspen stands I studied. Similar changes often accompanied by increased density of vegetation that may further hinder the establishment of deer sensitive trees, shrubs and herbs has been found in other forest communities (Ferns – Horsley et al. 1993b, George and Bazzaz 1999, Sedge – Randall and Walters unpublished date, Weigmann 2006). Management interventions in addition to decreasing deer populations may be needed to restore the composition and structure of affected stands and these interventions could be expensive (direct planting or seeding), time consuming (decades, not years, to restock stands), and/or socially unpopular (herbicides).

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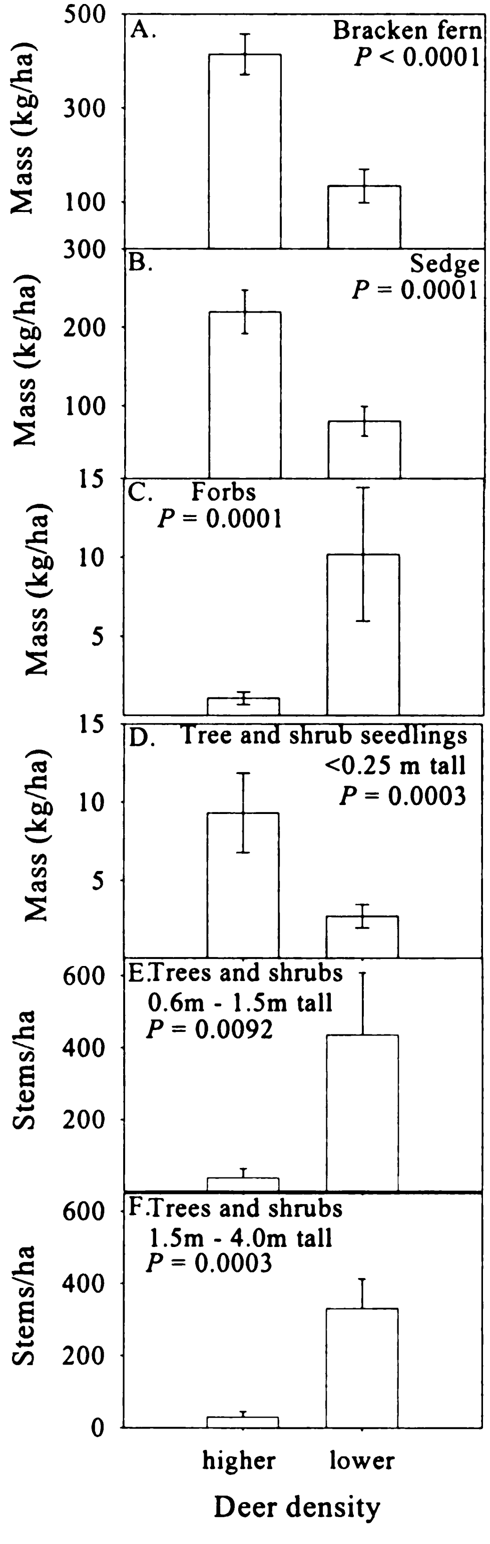

Figure 1.1. Mean biomass (± 1 SE) for bracken fern (2A), sedge (2B), herbs (2C), and seedlings (2D) and mean (± 1SE) # of seedlings stems (0.6m – 1.5m in height) / ha (2E), and mean (± 1SE) # of seedlings stems (1.5m – 4m in height) / ha (2F), for lower and higher deer density areas.

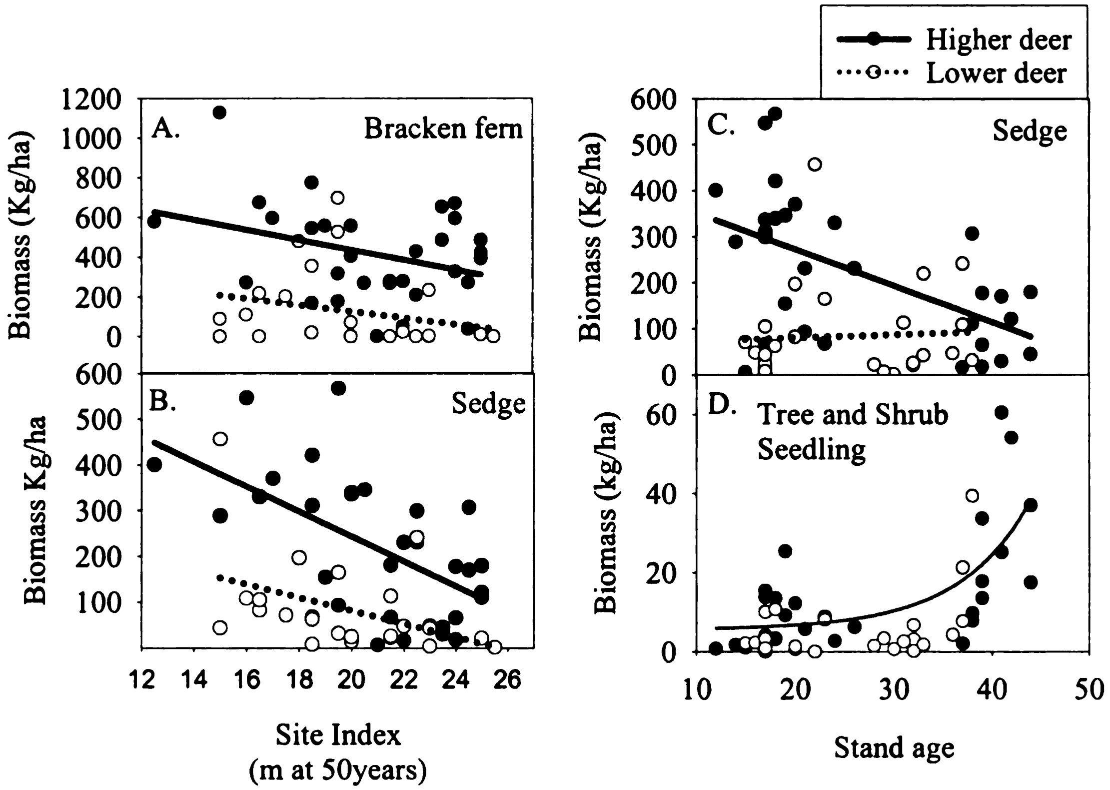

Figure 1.2. Higher and lower deer density average bracken fern (2A) and sedge (2B) biomass and their relationship to site index, as well as higher and lower deer density average sedge biomass and its relationship to stand age (2C). Seedling biomass (2D) vs. stand age.

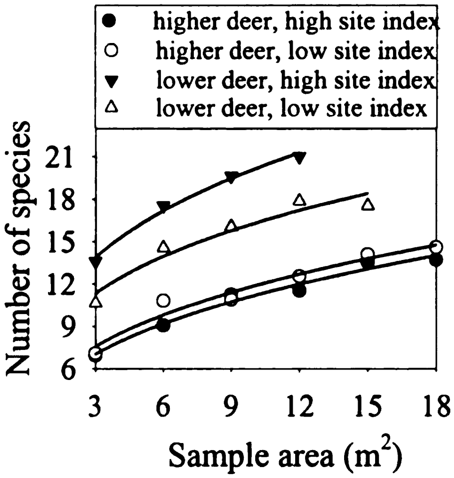

Figure 1.3. Species per unit area sampled by deer density (lower and higher and site productivity (low and high) categories.

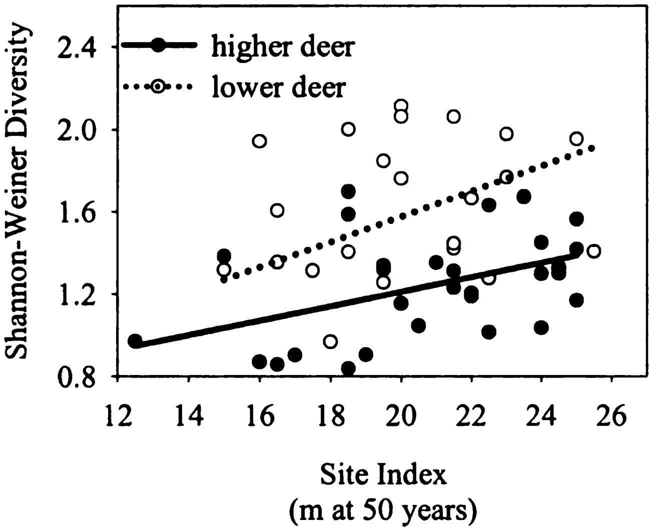

Figure 1.4. Shannon-Weiner diversity indices across site productivity gradients in Lower vs. Higher deer density areas. Higher deer densities areas did not show a relationship between SI and diversity while lower deer areas did. The overall least squared means were significantly higher in lower deer areas (1.7) verses higher deer areas (1.24).

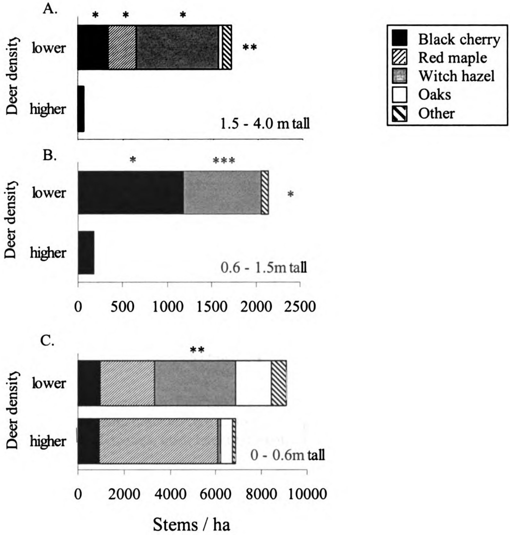

Figure 1.5. Stems/ha for a select group of species (black cherry, oak, red maple, witch-hazel, and a combined group "other") by deer density (lower & higher). All stands represent a uniform subset of stands by age and site index. Symbols (* and **) at the end of the columns represent significantly different (P=0.0247 and P=0.0060 respectively) mean total stems/ha between lower vs. higher deer density areas. Symbols *, **, & *** above column represent significant differences (P=0.05, P=0.001, and P<0.0001 respectively) within an individual species between higher and lower deer density.

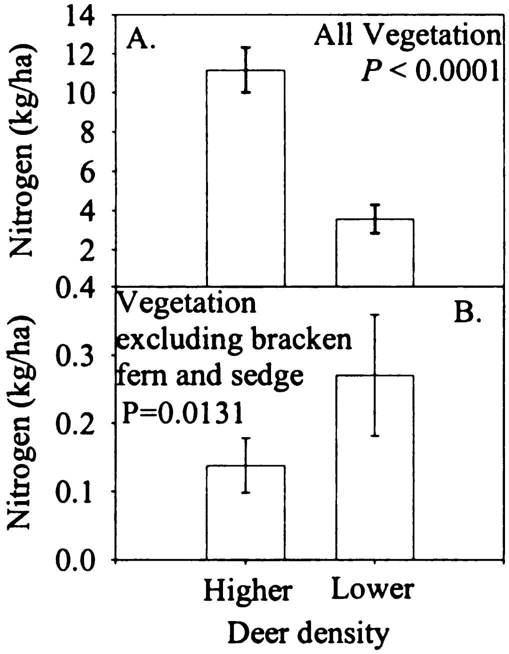

Figure 1.6. Total vegetation nitrogen (kg / ha) (Fig. 6A) and vegetation nitrogen (kg / ha) excluding bracken fern and sedge (Fig. 6B) in areas with lower and higher deer densities. error bars represent ± 1SE.

Appendix 1.1. Results of a standard least squares mixed model for the effects of deer density, site index, stand age and their interactions on bracken fern, sedge, forb, seedling < 25 cm, and # of stems/ha (0.6m – 4m). Interactions with P > 0.25 were pooled with the error term (Bancroft 1964) and the models rerun.

Vegetation biomass	Anova Effects	SS	F	P
A- Bracken Fern	Deer	1265504.6	28.162	**<0.0001**
	Site index	281524.9	6.2648	**0.0155**
	Age	1421.7	0.0316	0.8595
	DxSI	102150.6	2.2732	**0.1377**
	Adj. R^2			0.3399
B- Sedge	Deer	24.642	23.42	**<0.0001**
	Site index	3.293	3.13	0.0831
	Age	1.2804	1.22	0.2754
	DxA	4.436	4.22	**0.0454**
	DxSI	4.655	4.42	**0.0406**
	SIxA	1.823	1.73	0.1942
	Adj. R^2			0.4242
C- Forb	Deer	1275.25	32.26	**<0.0001**
	Site index	11.013	0.2786	0.5999
	Age	147.46	3.731	0.0589
	DxSI	184.99	4.6799	**0.0351**
	Adj. R^2			0.3831
D- Seedling (<0.25m)	Deer	494.266	14.153	**0.0004**
	Site index	27.897	0.799	0.3756
	Age	611.221	17.502	**0.0001**
	DxSI	198.096	5.672	**0.0209**
	Adj. R^2			0.4500

Appendix 1.2. Results of a standard least squares mixed model for the effects of deer density, site index, stand age, and their interactions on seedling stem density by height class and Shannon-Weiner diversity indices. Interactions with P > 0.25 were pooled with the error term (Bancroft 1964) and the models rerun.

Stem density	Anova Effects	SS	F	P
A- stems (0 to 0.6m) / ha	Deer density	3144604.5	1.4722	0.2466
	Site index	9969228.6	4.6672	0.0500
	Age	5661015.1	2.6502	0.1275
	AxSI	7716521.6	3.6125	0.0797
	Adj. R^2			0.3050
B- stems (0.6m to 1.5m) / ha	Deer density	1221202.9	6.3286	**0.0247**
	Site index	87107.4	0.4514	0.5126
	Age	136451.5	0.7071	0.4145
	Adj. R^2			0.1669
C- stems (1.5m to 3.99m) / ha	Deer density	317104.9	10.7297	**0.0060**
	Site index	47923.3	1.6215	0.2252
	Stand Age	39779.9	1.346	0.2668
	Adj. R^2			0.4344
D- Understory forb Shannon – Weiner Diversity Index	Deer density	2.793	30.65	**<0.0001**
	Site index	1.295	14.208	**0.0005**
	Stand Age	0.0019	0.2086	0.6504
	DxA	0.173	1.902	0.1757
	AxSI	0.559	6.138	**0.0177**
	Adj. R^2			0.5075

Appendix 1.3. Results of a standard least squares mixed model for the effects of deer density, site index, and their interactions on species richness at a defined area ($3m^2$, $6m^2$, $9m^2$, and $12m^2$).

Sampling Area	Effect	SS	F	P
$3m^2$	Deer	655.4	64.5	**<0.0001**
	Site index	49	4.8	**0.0305**
	DxSI	60.8	5.99	**0.0162**
$6m^2$	Deer	936.4	70.9	**<0.0001**
	Site index	9	0.6817	0.411
	DxSI	139.2	10.547	**0.0016**
$9m^2$	Deer	1149.2	161.3	**<0.0001**
	Site index	98	13.76	**0.0003**
	DxSI	65.6	9.21	**0.0031**
$12m^2$	Deer	1369	240.8	**<0.0001**
	Site index	29.2	5.1	**0.0258**
	DxSI	108.2	19.023	**<0.0001**

Appendix 1.4. Results of a standard least squares model for the effects of deer density, stand age, and site productivity by species (Black cherry, Red maple, and Witch-hazel) on seedling stem density by height class. Interactions with P > 0.25 were pooled with the error term (Bancroft 1964) and the models rerun.

Stem density	Species	AOVA effects	SS	F ratio	P
A- stems (0-0.6m)	Black cherry	Deer	123032.2	0.0682	0.7984
		Site Index	508072.8	0.2815	0.6054
		Stand Age	1459679.2	0.8088	0.3862
		Adj. R^2			-0.1191
	Red Maple	Deer	60385	0.0047	0.9463
		Site Index	42442731	3.3319	0.0952
		Stand Age	5817354	0.4567	0.5131
		Adj. R2			0.1097
	Witch hazel	Deer	47540168	5.6163	**0.0354**
		Site Index	8725328	1.0308	0.3300
		Stand Age	3103245	0.3666	0.5561
		Adj. R2			0.2161
B- stems (0.6-1.5m)	Black cherry	Deer	17118.6	0.1951	0.6720
		Site Index	302551.8	3.4479	0.1057
		Stand Age	1036328.4	11.8099	**0.0109**
		DxA	727317.4	8.2885	**0.0237**
		DxSI	353571.7	4.0293	0.0847
		AxSI	279529.7	3.1855	0.1175
		DxAxSI	312804.4	3.5647	0.1010
		Adj. R2			0.7455
	Red Maple	Deer	No red maple stems found in this class		
		Site Index			
		Stand Age			
		Adj. R2			
	Witch hazel	Deer	3424564.7	23.99	**0.0005**
		Site Index	935.8	0.0066	0.9369
		Stand Age	566160.1	3.9665	0.0718
		DxA	582961.6	4.0842	0.0683
		Adj. R2			0.6247
C- stems (1.5 - 3.99m)	Black cherry	Deer	266185.2	4.885	**0.0442**
		Site Index	33178.3	0.6089	0.4482
		Stand Age	79.9	0.0015	0.9700
		Adj. R2			0.1725
	Red Maple	Deer	153491	5.985	**0.0308**
		Site Index	11172	0.4356	0.5217
		Stand Age	13097.7	0.5107	0.4885
		Adj. R2			0.1815
	Witch hazel	Deer	3745214.8	6.9746	**0.0204**
		Site Index	650234.9	1.2109	0.2911
		Stand Age	366219.7	0.6820	0.4238
		Adj. R2			0.2229

Appendix 1.5. Results of a standard least squares mixed model for the effects of deer density, site index, stand age and their interactions on total vegetation N, forb and seedling N, bracken % N, sedge %N, herb % N, seedling leaf % N, seedling stem %N. Interactions with P > 0.25 were pooled with the error term (Bancroft 1964) and the models rerun.

Vegetation nitrogen	Effect	SS	F	P
A- Total vegetation N	Deer	27.94	33.09	**<0.0001**
Kg N/ha	Site index	1.108	1.312	0.2572
	Age	0.7437	0.8808	0.3523
	SIxA	1.3558	1.606	0.2107
	Adj. R^2			0.3916
B- Forb & Seedling	Deer	9.233	6.255	**0.0157**
Kg N/ha	Site index	10.093	6.838	**0.0118**
	Age	11.783	7.983	**0.0068**
	Adj. R^2			0.2703
C- Bracken % N	Deer	0.00003	0.0003	0.9859
	Site index	0.8068	7.8219	**0.0077**
	Age	0.3339	3.2372	0.079
	Adj. R^2			0.1252
D- Sedge % N	Deer	0.0020	0.0406	0.8411
	Site index	0.7842	15.818	**0.0002**
	Age	0.0779	1.5724	0.2154
	Adj. R^2			0.1903
E- Forb %N	Deer	0.0281	0.2524	0.6189
	Site index	0.5815	5.2217	**0.0293**
	Age	0.2057	1.847	0.1839
	DxSI	0.0927	0.8323	0.3686
	DxA	0.3165	2.842	0.1019
	SIxA	0.7443	6.684	**0.0147**
	DxSIxA	0.7046	6.327	**0.0173**
	Adj. R^2			0.3134
F- Seedling Leaf % N	Deer	0.0367	0.7392	0.3944
	Site index	0.0006	0.0119	0.9137
	Age	0.4833	9.7359	**0.0031**
	DxSI	0.2974	5.9912	**0.0183**
	SIxA	0.3382	6.8130	**0.0122**
	Adj. R^2			0.1939
G- Seedling stem %N	Deer	0.0106	0.3979	0.5319
	Site index	0.0094	0.3534	0.5556
	Age	0.1634	6.1151	**0.0179**
	SIxA	0.0934	3.5001	0.0689
	Adj. R^2			0.1143

CHAPTER 2

SEPARATING DEER BROWSE AND SEDGE EFFECTS ON UNDERSTORY VEGETATION DYNAMICS IN TEMPERATE NORTHERN HARDWOOD FORESTS.

Executive summary

High deer populations since the mid 1970's in Michigan's central Upper Peninsula have coincided with increased abundance of non-browsed or browse resistant species such as upland sedge (*Carex pensylvanica* Lam.) and ironwood (*Ostrya virginiana*), and a decrease in browse preferred tree seedlings and saplings (e.g. sugar maple). It has been shown in systems that non-browsed species may persist, even if deer are removed, by outcompeting browse sensitive species for resources, yet little is known if the vegetation pressures from non-browsed species are additive to the pressures associated with deer or if the non-browsed species pressures have become the primary driver of failed regeneration in the system. I attempted to answer if deer , sedge, or deer + sedge pressures are driving the vegetation and structural shifts found in areas with elevated deer densities and widespread sedge covers. I separated deer and understory vegetation (predominantly sedge) effects on vegetation-resource dynamics in selection harvested stands with high (> 20 km^2) long-term deer densities with experiments that included vegetation manipulations (all understory vegetation removal, vegetation removal plus scarification, sedge removal, control) and deer treatments (exclosures/open)

After four years of deer exclusion and/or vegetation manipulation it was clear that deer not sedge populations were driving most of the responses that I measured. Areas protected from deer had significantly higher coverages of deer sensitive species

(*Mianthemum canadensis*, *Trillium grandiflorum* etc) while areas open to deer had greater coverages of "weedy" species (dandelion, goldenrod) and browse tolerant *Carex.*

Deer effects on forest structural characteristics were clearly demonstrated as well, as no seedling of any species grew to a height that was above the reach of deer over the course of this study 4 years. Naturally established sugar maple seedlings were hardest hit, being eliminated above 0.25 m in areas open to deer, while planted sugar maple seedling growth was reduced by ~1/3. Deer even reduced or outright eliminated ironwood seedlings above 100 cm.

Although deer were primarily responsible for declines in seedling growth via browsing, vegetation (mostly sedge) also reduced seedling height and mass, especially at higher light levels and this was possibly driven by differences in soil moisture resources found between areas with and without sedge. I found no evidence that deer or treatments altered extractable inorganic N or rates of nitrogen mineralization.

This study does show that current deer densities are too high for canopy recruitment of northern hardwood regeneration. If or when deer numbers decline, the time needed for seedlings to grow above the browse zone can be reduced (by 6-10 years) to approximately 8-10 years if sedge competition is controlled. More work is needed to economically control sedge in an ecologically friendlier manner to minimize effects to forbs, desired seedlings, and fauna in the understory.

Introduction:

Compared to non-selective disturbance agents such as fire, landslides, windthrows, and ice storms, large-scale ungulate herbivory may be a unique form of disturbance (Hulme 1996). Ungulates are highly selective in the plants they consume (Swift 1948, Crawley 1990, McInnes et al., 1992, Cornett et al., 2000, and Jefferies et al., 1994) and as such, at high densities, large ungulates (e.g. deer, elk, moose) can alter plant species composition by selectively foraging on highly palatable species while ignoring species of low palatability (Coughenour 1991, DeCalesta 1997, Horsley et al., 2003, Randall chapters 1). For plants browsed by ungulates, the direct losses associated with the removal of biomass can be compounded in subsequent years as browsed plants alter growth (increased shoot growth – McNaughton 1983, Danell et al., 1985, Bergstrom and Danell 1987, Campa 1989, and Molvar et al., 1993), regrowth nutrient status (higher foliar N – Du Toit et al., 1990) and secondary defense levels (lower tannin and/or lignin levels - Du Toit et al., 1990) increasing the potential for future browsing events (Danell et al., 1985) Conversely, some browsed species lower their aboveground mass and foliar N concentrations in response to browsing while increasing root growth and secondary defense levels (ether extracts – Campa 1989). As such, sustained (seasonally repeating) high browsing pressure on seedlings can cause differing responses. In some instances trees may survive the browsing events but be chronically deformed (shrub formation vs. single dominant stem)(Gill 1992), while others that succumb to browsing result in outright tree recruitment failure (Tilgham 1989, Randall Chapter 1) which overtime, can lead to decreased vertical structure complexity (Horsley et al., 2003, Russell et al., 2001, Randall Chapter 1) and loss of intermediate forest canopy layers. Chronic browsing has also been shown to alter nutrient cycling regimes (Pastor et al., 1993, Pastor and Cohen 1997), and vegetation species richness (increase - Raymer 2001 or decrease - Frelich and Lorimer 1985, Chapter 1). Increased richness in high deer areas is usually synonymous with an increase in "old field" species (Milchunas and Lauenroth 1993, Raymer 2001) driven primarily by increased light resources reaching the understory caused by deer induced thinning of the overstory. In closed canopy forests (lower light levels), deer directly remove preferred understory species, which are usually replaced by a single dominant browse resistant or non-browsed species that is tolerant of intermediate to lower light levels.

The presence/absence of deer browse sensitive herbaceous plants (*Clintonia borealis* (Ait.) Raf, *Aralia nudicaulis* L. [Balgooyen and Waller 1995], *Maianthemum canadensis* Desf. [Balgooyen and Waller 1995, and Rooney 1997, 2001], *Osmorhiza claytonia* (Michx), *Arisaema triphyllum* (L) Schott., and *Actaea pachypoda* Ell. [Webster and Parker 2000], *Smilacina racemosa* L. and *Uvularia* spp. L. [Fletcher, et al., 2001] and *Trillium* spp. L. [Augustine and Frelich 1998]) are often used as indicators of deer-browsing pressure.

In Michigan's central Upper Peninsula (Menominee County averages for '57-'75 & '76-'99 were 15.8 and 31.3 deer/km^2, respectively, from Michigan DNR fecal pellet count data obtained from Bob Doepker) increased second growth timber harvesting resulted in a sharp increase in deer population numbers in the mid 1970's as deer numbers responded to increased preferred browse. These high deer population areas are increasingly found to be in close association with highly managed northern hardwood stands that have understories dominated by browse resistant, disturbed- canopy loving

Carex pensylvanica Lam. (Pennsylvania sedge). Although the observed high sedge densities have been linked to high deer densities areas (International Paper management records, Chapter 1, Horsley 1993, Weigmann 2006), other factors such as invasive earthworms (Hale et al., 2006), and selection harvesting practices (Metzger and Schultz 1984, Horsley 1990, but see Jenkins and Parker 1999) may also be important in the establishment of sedge and the reduction in regenerating seedlings. Regardless of the cause of high sedge densities, *Carex* spp. have been found in other systems to be strong competitors with vegetation, including tree seedlings. Thus it is possible that both deer and sedge affect understory vegetation dynamics, including those of juvenile trees

In northeastern hardwood systems, vegetation changes caused by deer have been hypothesized to persist (i.e. are stable) even if deer are removed. In these systems, established non-browse preferred species may have self-reinforcing mechanisms that suppress reinvasion of browse-preferred tree and shrub seedlings and forbs independent of the direct deer effects (Stromayer and Warren 1997, Augustine et al., 1998, de la Cretaz and Kelty 2002, George and Bazzaz 1999). The thick sedge documented in managed northern hardwood stands could represent an alternate stable vegetation state, maintaining understory dominance perhaps, by it being a strong competitor for nutrients, water and/or space.

In this study, my goal was to separate deer and understory vegetation (predominantly sedge) effects on vegetation and resource dynamics in selection-harvested stands with high (> 20 km^2) long-term deer densities. My experiments focused on the effects vegetation manipulations (all understory vegetation removal, vegetation removal plus scarification, sedge removal, control), deer treatments (exclosures/open) and their interaction on understory vegetation dynamics. Specifically, I asked, 1) what are the relative impacts of sedge-dominated understories and deer on tree seedling establishment, survival and growth, and forb diversity?, 2) If deer and understory vegetation affect growth, are these effects associated with soil nitrogen and water availability, and 3) if there are effects of vegetation on growth and survival, how do these effects vary with light availability?

Methods:

Field Experiments

***Location*:** I have two field experiments, both of which are located on land formerly owned and managed by International Paper (IP) in Menominee County, Michigan. Stands are classified as upland northern hardwoods dominated by sugar maple (*Acer saccharum* Marsh), with white ash (*Fraxinus Americana* L.), basswood (*Tilia americana*), bitternut hickory (*Carya cordiformis* (Wang.) K. Koch), black cherry (*Prunus serotina* Ehrh.), and hop hornbeam (*Ostrya virginiana* (Mill.) K. Koch) also being found on the sites. These forests have been selectively harvested at 8-12 year intervals for approximately 50 years, Typically each selective harvest entry reduced basal area from approximately 25.3-27.6 m^2/ha to approximately 17 m^2/ha. (For stand characteristics and histories per replicate study site see Appendix 1). Despite post-harvest conditions that should favor it, there has been little recruitment of *Acer saccharum* saplings from seedling classes for over 30 years (Mike Young, IP, personal communication). Sedge (mostly *Carex pennsylvanica*) comprises over 80% of herb layer biomass in these stands (Randall and Walters, unpublished data, field observation over last five years). The five main study sites are on five different drumlins (< 3 km from one another), which are part of the Northern Lake

Michigan (Hermansville) Till Plain, with soils being moderately to well-drained spodisols and alfisols (Albert 1995) (For detailed belowground descriptions per replicate site see Appendix 2). Drumlin parent material (dolomite and limestone) is generally within 9.1 – 15.2 m of the surface (Albert 1995). The relatively mild winter climate, along with the landscape vegetation structure (hardwood dominated drumlins used for browse interspersed with lowland cedar swamps used as thermal protection in winter) creates conditions favorable for supporting high winter deer populations.

Experimental designs

In summer 2000, with assistance from International Paper researchers and land managers I filtered their stand inventory database and created a list of potential stands that were characterized as 1) dominated by sugar maple with trees already in the sawlog class (IP's M6 designation), 2) was recently (within 2-3 years) harvested with single tree or small group selection cuts (2-3 trees maximum) and were therefore not eligible for reentry within an 8-10 year research window, 3) were harvested to reduce BA to $17 m^2/ha$, and lastly, were located on IP land holdings in Faithorn Township, Michigan. Potential stands were visually inspected for topographic consistency, as well as stand overstory composition, structure, and basal area retention. I selected five replicate drumlin sites (each site was a single stand) and established on each a 400 m^2 fenced (to 2.6 m height) deer exclosure paired at close proximity with a 400 m^2 unfenced area, all five exclosures and paired open areas were centered under harvest gaps (1-2 dominant/co dominant trees removed). All 400 m^2 fenced and unfenced areas were split into four 10 x 10 m treatment plots that received one of four randomly assigned vegetation manipulations in mid-August 2000. These were: all vegetation killed with glyphosate herbicide followed two weeks later by a mechanical soil scarification treatment to expose mineral soil (Herbicide + Scarification), all vegetation killed with glyphosate with no scarification (Herbicide), weeding of sedge only (to mimic a sedge-specific herbicide)(Selective), and a control. Although effective in promoting seedling establishment in many regions, scarification alone was not used as a treatment since an earlier industrial trial indicated that it was ineffective at decreasing sedge and increasing tree seedling densities (Mike Young, International Paper, personal communication). Prior to setup, subplots were randomly assigned in the lab and tagged in the field to various measurements (10 subplots / treatment / year (2000, 2002 and 2004) for % cover estimates and destructive biomass harvests, 10 subplots / treatment for planted seedlings (five for sugar maple, five for white ash), 10 subplots / treatment to quantify and track naturally establishing seedling cohorts in 2001 and 2002). No subplot was ever reentered after a destructive harvest.

To ensure adequate numbers of experimental tree seedlings, I supplemented naturally establishing seedlings by planting two-month-old greenhouse raised sugar maple and white ash germinants into 10 subplots (five subplots received five sugar maple, five subplots received five white ash) in each treatment replicate in 2001. Seed was collected from a Western New York site (USDA hardiness zone 4b) for sugar maple, and white ash was purchased from Sheffield seed company in NY (collected from USDA Hardiness zone 4b). Seed was stratified in a cold room following the protocol in Young and Young (1992). Seedlings where raised in the greenhouse at Michigan State University's Tree Research Station before being transported to the field sites where they were immediately planted.

It is widely known that increased canopy openness conditions (a proxy for light availability) can alter seedling survival, growth, (Walters and Reich 1997, Beaudat and Messier 1998) and competition pressures for resources from surrounding vegetation (Davies et al. 1999). Because all treatment areas (described above) were in a fairly narrow range of light levels (~ 6.5-11 % of open sky measurements explained below) when the larger Deer/No Deer [nested treatment] study began, I located 60 pairs of two-year old naturally established sugar maple seedlings within the general study area in mid September 2000. These 60 pairs were distributed over a broader range of light levels (1-22 % canopy openness measured with an LAI 2000 at a point 10 cm from the seedlings apical bud) enabling me to quantify if sedge affects seedling growth and survival disproportionately as light levels change. All seedlings had an exclosure constructed with field fence (1m radius x 122 cm tall) to protect from deer and one seedling from each pair had all vegetation (primarily sedge) removed from within a 1 m radius by hand. A follow-up spray application of Glyphosate (rate of 1quart/acre) the following growing season removed all returning vegetation.

Measurements:

Vegetation cover, diversity, seedling densities, and vertical structure

Tree seedling and other vegetation measurements (destructive and non-destructive) were first taken prior to treatment in summer 2000 and culminated with final measurements taken in summer 2005. In 2000, 2002, and 2004 two observers simultaneous estimated % cover occularly for each species in 10-1m^2 subplots / treatment area. Ocular estimates were then averaged, recorded and Shannon-Weiner diversity estimates were derived using the equation $\{\Sigma \text{ Pi} * \text{LogPi}\}$. Seedlings <25cm in height were counted and estimated % cover was obtained by species. At the same time, woody plant vertical structure (height distribution of woody stemmed plants) was obtained by measuring all seedlings (woody stems > 25cm but less than 1.45 m). Seedling heights were recorded to the nearest 10cm height class (0.25m –0.35m, 0.35m-0.45m…) by species. Because Herbicide and Herbicide + Scarification treatments killed all advanced regeneration at the outset of this study, and because of the limited seed fall into the sites, future vertical structure development was hypothesized to be severely impacted over the course of this study. As such, I limited vertical structure development results to Control and Selective treatments. Ironwood (*Ostrya virginiana*) was uniformly the dominant tree species in the seedling layer across all sites at the beginning of the study, structural results for this species represent data from all five replicate sites. Sugar maple is also represented but only two of the 5 sites are used as the remaining 3 had little to no advanced regeneration prior to the study. In 2004, concerned with the low numbers of sugar maple seedlings actually measured in the 10 subplots / treatment, I sampled the remaining 34 unharvested subplots on each site, which were set aside for longer-term measurements. Individuals in the 34 extra subplots were remeasured in 2005 to obtain growth from '04-'05. I non-destructively monitored planted sugar maple and white ash seedling survival on a monthly basis from May through October in 2001 and then semi annually (spring and fall) from 2002-2004.

Vegetation biomass and N content

In 2000, 2002, and 2004 I destructively harvested aboveground vegetation in the core area (0.5 x 0.5 m) from the 10 1-m^2 sub-plots / treatment area used to obtain % cover by species. Destructive measurements provided a more robust data set, in that, occularly estimated % cover data collected in 2000, 2002, and 2004 may have been unintentionally biased in Controls due to heavy sedge cover. Harvested vegetation was separated in the field into one of eight categories (forbs, sedge & grass, tree seedling leaves and stems, recruit seedling leaves and stems below 25 cm, and recruit seedlings leaves and stems> 25cm). For clarification, a recruit seedling is and individual that is greater than 25 cm tall but less than 1.45m tall. The sedge and grass category was dominated (> 90%) by *Carex pensylvanica* Lam. and will hereafter be called sedge. All samples were dried at 70°C for 72 hours in the lab prior to measuring dry mass. All dried samples were passed through a Wiley mill, pulverized in a hammer mill (KLECO – Kinetic Laboratory Equipment Company, Visalia, CA) and analyzed for N concentration by the Dumas combustion method with a CHN analyzer (Carlo Erba, Milan, Italy).

All sugar maple individuals were harvested from the 60 pairs across an openness gradient in early fall 2004. Seedlings were harvested by clipping at the root collar, aboveground parts were stored in ziplock bags, transported to the lab at MSU, and were evaluated for total height growth prior to drying at 70 C for 72 hours at which time dry mass was then obtained.

Light and soil resource measurements

I measured canopy openness (a proxy for light) in 2001 at 16 evenly distributed points (each sampling point touched the corners of 4 unique subplots ensuring all 64 subplots in the core area had an associated openness measurement) in each of the treatment core areas (8 x 8 m) within the Deer/No[nested treatments] with a dual LAI 2000 (LiCor Inc., Lincoln NE) setup. Both instruments were placed side by side for calibration of the optical sensor in an open field where there would be no interference from trees (setup at least 3X the canopy height away from the forest / field edge. One LAI sensor and data logger was left in the open to continuously measure and log total potential canopy openness, while the other LAI unit was taken to measure openness levels under the canopy in each treatment. In the lab, data was transferred to a computer, and the C2000 (program provided by LiCor) was used to synchronize time stamps and calculate canopy transmittance (openness) as differences in total potential open sky verses measurements collect under the canopy which intercepts a certain level of the total potential transmittance at each site. Canopy openness (same LAI 2000 protocol as above) was also measured at 1m above each of the 60 pairs (n=120) of naturally established sugar maple seedlings, where half had vegetation removed and half were vegetated controls.

Nine, one month long *in situ* incubations were used to measure soil inorganic nitrogen(for dates of incubations see Table 2.8). I randomly punched eight pairs of soil cores in each treatment area and immediately pulled one from each pair. The remaining eight cores were incubated *in situ* for 30 days and the following extraction procedure was used for both initial and final incubation samples. All eight pulled cores per treatment were sieved to pass a 4 mm screen in the field, thoroughly homogenized, subsamples were stored in ziplock plastic bags, refrigerated @ 1°C, and transported to the lab. Soils were extracted within 48 hours with 2M KCl (20g field moist soil with 50ml KCl) on a shaker table for one hour, and allowed to settle for 30 minutes before being filtered through Whatman® #42 filter paper. Soil moisture was determined gravimetrically at the time of each extraction to allow calculation of NO_3^--N and NH_4^+-N on a per unit dry soil basis. All extracts were refrigerated until being measured for NH_4^+-N and NO_3^--N (measured within 30 days of extraction) on an OI Alpkem Autoanalyzer (OI Analytical, College Station, TX) by phenol-hypochlorite and cadmium reduction methods, respectively. I expressed inorganic extractable N (NO_3^--N and NH_4^+-N) on a gram N / gram dry soil basis. Rates of N-mineralization were calculated as the change in inorganic N ($NO_3^- + NH_4^+$) on a dry soil basis from initial to final measurements {(Final $NO_3^- + NH_4^+$) - (Initial $NO_3^- + NH_4^+$) / incubation period (days)}

Soil moisture measurements (15 over the course of the four growing seasons see Table 2.6) were a combination of the nine initial moisture measurements collected from the initial *in situ* N measurements and six measurements determined gravimetrically from punched soil cores randomly taken in each Deer / No Deer treatment. Soil cores were also punched to obtain gravimetrically determined soil moisture content around each of the 60 pairs of seedlings at 11 measurement dates (see table 2.7).

Analysis:

Prior to setup, the four treatments (Control, Herbicide, Herbicide and Scarification, Selective) were randomly assigned to one of the 10 x 10m vegetation manipulation treatment areas within each of the Deer / No Deer treatments in each of the five replicates (sites). For analysis, vegetation manipulation treatments were nested within Deer / No deer treatment and denoted as Deer / No Deer [treatment] throughout the paper. To analyze vegetation mass, N content, diversity, and structural change over time I included year as a factor in initial ANOVA model with main effects Deer / No Deer and Deer/No Deer [nested treatment] effects. Subsequent models were rerun to test Deer / No Deer and Deer/No Deer [nested treatment] effects within a given year. Tukey-Kramer HSD was used to test for significant differences ($P<0.05$) among years and then for treatments within Deer / No Deer. If nested treatments were not significantly different (P>0.05) the model was reduced and Deer / No Deer effects were tested with Student's T tests. For soil resources (extractable N, N mineralization rates, and soil water) tests were similar to above models (least squares models) with the only difference being Year was not added to the initial model.

Because established seedlings influence, to a great degree, the advanced regeneration layer in future years, I limited most of the vertical structure tests to Control and Selective treatments (the two herbicide treatments killed all advanced regeneration at the outset of the project). For both ironwood and sugar maple advanced regeneration stem densities, initial ANOVA tested vertical height class (nominal), Deer / No Deer [nested treatment] effects. For each species, nested vegetation treatment effects were not significant in the model and were reduced to just Deer / No Deer treatments. Deer / No Deer effects on stem densities were tested by individual height class with Student's T tests.

Using Deer / No Deer and Deer / No Deer[vegetation treatments] as covariate predictors, I model planted seedling survival with Cox's proportional hazards methods (Cox 1972) in JMP 5.1 statistical software (SAS Institute, Cary, NC, USA). Deer had such an overwhelming effect on planted seedling survival and growth that I restricted analysis of growth to only those seedlings in exclosures. Inside exclosures, growth was analyzed with least squares regression in mixed models with main effects of canopy openness (continuous), treatment (nominal) and their interaction. If model results indicated that the interaction term was insignificant beyond the threshold suggested for pooling variances (P > 0.25, Bancroft 1964), the interaction term was removed and the model was re-run.

In the small companion study, treatment (vegetation/vegetation removed – Nominal variable), % canopy openness (continuous), and their interaction effects on naturally established sugar maple seedling growth, stem mass and soil moisture resources were tested using least squares regression in JMP.

Results

Vegetation Biomass

Two years after vegetation treatments (2002), Selective, Herbicide and Herbicide + Scarification treatments had much lower sedge biomass than controls in both Deer (average, 99.7% reduction) and No Deer (94.1% reduction) treatments (Figure 2.1A & B, Table 2.1A). In 2004, sedge biomass had started to rebound but was still, on average, 50-55% lower in the three vegetation manipulation treatments than in the Control. There was a trend in both 2002 and 2004 for greater sedge mass in Herbicide + Scarified than in the Herbicide treatment.

Forb mass was unaffected by vegetation treatments (Figure 2.1, Table 2.1). In contrast, forb mass was 50 % lower in Deer than No Deer treatments, but only in 2002, as forb mass rebounded to Control levels by 2004 in these Deer areas. Although deer had modest and temporary effects on forb mass in vegetation manipulation treatments, they had greater and more lasting effects on forb composition. In 2004, compared to the Deer treatment, the No Deer treatment had greater coverages of the following deer sensitive forb species (control treatment only): *Maianthemum canadensis* (700%), *Dentaria* (243%), *Trillium grandiflorum* (233%), *Uvularia grandifolia* (117%), and *Ozmorhiza* *claytonia* (95%), and tree species: *Acer saccharum* (79%). In addition, flowering trillium density was significantly greater in No Deer treatments (2965/ha vs. 45/ha). In contrast to No Deer treatments, Deer treatments had greater forb coverages of *Carex pedunculata* (447%), *Ribes* (200%), *Taraxicum officinale* (120%), *Solidago* spp. (100%), *Rubus hispidus* (100%) and *Carex pensylvanica Lam.*(32%), and seedlings coverages of *Abies balsamea* (50%), *Acer rubrum* (100%), and *Fraxinus americana* (173%). In 2002 and 2004 the Selection treatment had the highest H' diversity, the Controls the lowest, and the Herbicide and Herbicide + Scarification treatments were intermediate (Figure 2.3A, Table 2.1E). Deer/No Deer treatments had no effect on H' diversity.

In Herbicide and Herbicide + Scarification treatments seedling mass was 98% lower than in Control and Selective treatments in 2002 (Figure 2.1E & F, Table 2.1C), but by 2004, seedling mass had rebounded and differences among vegetation treatments were marginal (Table 2.1, P=0.0584). In the ten 1-m^2 subplots I found no recruit seedlings (seedlings > 25cm) in any of the replicate sites in 2000. Harvests in 2002 and 2004 resulted in so few recruit seedlings being harvested in Control and Selective treatments (none were harvested from the Herbicide and Herbicide + Scarification treatments) that we do not present them here.

Vegetation N content

As one might expect, vegetation N content (kg N/ha) tracked overall mass. Prior to vegetation manipulation treatments, no differences were found for sedge, forb, or seedlings <25 cm N content between Deer / No Deer treatments and their respective nested vegetation manipulation treatments (Figure 2.2, Table 2.2A,B, & C). In 2002, system-wide N content was 90-98% lower for sedge, but was again driven by the 94-97.7

% lower mass due to my vegetation manipulation treatments (Figure 2.2A & B). By 2004, sedge N content was 54-60% lower than controls, which again follows the roughly 50% lower sedge mass.

Forb N content in 2002 was highly variable among vegetation treatments in the Deer treatment, but overall, N content was roughly 50% of that found in the No Deer treatment. By 2004, forb N content levels were not significantly different, but did parallel the large increase in forb mass (6.53X) from 2002 to 2004, increasing forb N content by ~5.85X (Figure 2.2C & D Table 2.2B).

Two years after treatment, seedling N content was consistently higher in Selective treatment areas than Herbicide and Herbicide + Scarification treatments. By 2004, large variation in seedling N content caused the Deer / No Deer [vegetation manipulation treatment] effect to not be significant (Table 2.2C). Like forb N content, seedling N content increased from 2002 to 2004 by over 7X (Figure 2.2E & F). Selective treatments had consistently higher N content in both Deer and No Deer treatments while Herbicide + Scarification had the lowest N content.

N Concentrations were unaffected by Deer / No Deer [Vegetation manipulation treatments] in 2000, 2002, and 2004 samples of sedge (2000 *P*=0.7799, 2002 *P*=0.8207, 2004 *P*=0.6093), forb (2000 *P*=0.4432, 2002 *P*=0.8619, 2004 *P*=0.7205), or seedlings < 25cm (2000 *P*= 0.5104, 2002 *P*= 0.4733, 2004 *P*=0.2366).

Planted seedling survival and growth

Averaged over all vegetation treatments, survival of planted sugar maple seedlings was 63% lower in Deer, than No Deer treatments (Figure 2.4A, Table 2.3A). Neither deer nor vegetation treatments affected white ash survival, and white ash had much greater survival than sugar maple (73.6% vs. 46.4% averaged across all treatments and Deer/No Deer areas) (Figure 2.4B, Table 3B).

Planted sugar maple seedlings were significantly shorter in Deer than No Deer treatments (Figure 2.5A, P<0.0001). In the No Deer treatment, seedlings had the greatest height growth in the most severe vegetation manipulation treatment (Herbicide + Scarification), and the least in the Control (*P*=0.0321). Stem biomass patterns were similar to those for height, with seedlings having significantly more stem mass in No Deer areas (Figure 2.5B, *P*<0.0001).

In the No Deer treatments, with increasing canopy openness planted sugar maple seedlings increased in height growth in Selective and Herbicide + Scarified treatments (Figure 2.6A), and increased in stem mass in all but the Control treatment (Figure 2.6B). White ash height growth also increased with canopy openness in Control and Herbicide treatments, while its stem mass increased with canopy openness in all treatments (Fig 6C & D). Over a broad range of light (1-22%), naturally established sugar maple height and mass showed similar results. Tree seedling growth (height and stem mass) increased as canopy openness increased especially in high light areas where sedge was removed. (Figure 2.7A & B).

Vertical structure

Vertical development of ironwood seedlings and saplings was not affected by treatment (Control and Selective) but deer reduced stems > 100 cm (Figure 2.8, Table 2.4). Deer significantly reduced '04-'05 growth across both Control and Selective treatments but only within the four height classes between 26 cm-150 cm (Figure 2.9A, Table 2.5). Interestingly, the loss in yearly growth attributed directly to deer was greater as seedlings increased their initial 2004 size. For example, if a seedling was 26-50 cm tall in 2004, the difference in '04-'05 growth between a Deer and No Deer raised seedling was 3.06 cm, while a 100-150 cm tall height class seedling would have a growth difference of 22.45 cm.

At the outset of the study, only two sites had advanced sugar maple regeneration in the seedling layer. Sugar maple was able to grow above 25cm but only in No Deer treatments and stem densities were highly variable above 25cm (Figure 2.8.). In No Deer treatments, sugar maple had lower yearly height growth and attained a maximum height class of only 51-75 cm in Control treatments, whereas, in Selective treatments sugar maple grew into the 151-200 cm height class (Figure 2.9B).

Belowground resource availability (soil moisture, N pools, N mineralization rates)

Weather station data from Spalding, Michigan (17 km from my sites) showed that 2000, 2002, and 2004 had growing season rainfall totals that exceeded the 50 year average, while 2001 and 2003 were the 6th and 2nd driest growing season totals, respectively, over the same 50 year period (data not shown). Soil moisture responses to Deer/No Deer and vegetation treatments were weak (Figure 2.10, Table 2.6). In contrast, soil moisture was generally lower for vegetation intact, than vegetation removed treatments for the naturally established sugar maple seedling experiment. (Figure 2.11, Table 2.7), and soil water generally increased with canopy openness in this study.

Except for one of the nine measurement dates, KCl extractable soil NO_3^- -N was not significantly affected by Deer / No Deer or vegetation treatments (Table 2.8). On this date (July, 2003), both Deer and No Deer Selective treatments and No Deer Herbicide treatments had similar and greater NO_3^- -N values than all other treatment combinations (data not shown). NH_4^+ -N differed only on July 2003 (Table 2.9) as well, with significantly higher values in No Deer Selective treatments than Deer Selective and all other treatments were intermediate

Extractable soil NO_3^- -N and NH_4^+ -N, generally increased over the course of the experiment (Figure 2.12) with the only deviations from this trend being lower values in summer 2001 and 2003 which coincided with drought events. N- mineralization rates did not differ among treatments for any of the dates (Table 2.10). N-Mineralization declined 49.82% as a whole over the course of the study (Figure 2.13) with most of the total decline occurring during the 2001 growing season.

Discussion

After four years of deer exclusion, results were similar to Milchunas and Laenroth (1993), Raymer (2000), and Weigmann (2006) in that areas open to browsing had altered understory vegetation compositions as evidenced by the increased old-field component (goldenrod, dandelion, *Carex* etc), while areas protected from deer had increased populations of browse sensitive species (*Mianthemum canadensis*, *Trillium grandifolia* etc). Deer induced compositional shifts did not result in changes to overall sedge, forb, or seedlings biomass below 0.25m. Vegetation manipulation treatments initially reduced biomass of sedge and seedlings but all rebounded to pretreatment levels within 4 years. Control (vegetation, primarily sedge) treatment diversity remained uniformly lower, not as a result of sedge overabundance altering the evenness factor in the equation (as I excluded sedge from the calculated diversity), but rather, I believe sedge dominates the understory at the expense of forbs and seedlings by its ability to survive periods of intense stress (Chapter 4).

Results were mixed pertaining to the impacts of sedge on seedling growth and survival. Planted white ash showed little response to both deer and vegetation, while planted sugar maple altered growth in some treatments and not in others. The larger study showed that both planted and naturally established sugar maple seedlings were capable of surviving and growing with sedge under average light levels, showing no reduction in growth when control (sedge dominated plots) and selective sedge removal (only sedge removed plots) treatments were compared. Sugar maple successfully grew into small sapling class stems but only where deer were excluded, as deer browsed all stems >0.25m, and where I did not treat the vegetation with herbicide (removing advanced seedling regeneration as well).

In contrast to the larger study site, results from the 60 pairs of seedlings distributed across a broader range of available light showed increased negative effects of sedge on seedling growth and mass as light increased. The fact that seedlings grew significantly taller in areas without competing vegetation is not a novel result, as this has been shown in many grassland and forested systems (Carter et al., 1984, Davis et al., 1998, Dodd et al. 1998, Elliott and White 1987, Knoop and Walker 1985, Löf 2000, Peterson and Maxwell 1987, Sands and Nambiar 1984). However, across a light gradient, the increased negative impacts of sedge on seedling growth could mean that in these selectively harvested stands sedge may, in fact, be increasing the successional period needed to obtain a full stocked canopy. The 60 pairs of seedlings did have access to greater soil moisture when vegetation was possibly explaining the increased seedling height growth and mass in vegetation removal plots (higher soil water) vs. intact vegetation plots (lower soil water)(Elliott and White 1987, Gordon and Rice 2000).

I found similar vegetation manipulation and deer effects for ironwood as ironwood stems grew equally well in both controls (sedge) and selective (no sedge) treatments and deer reduced or eliminated all ironwood stems above 100 cm. For all height classes where stems of ironwood were present, deer essentially standardized yearly growth, causing small seedlings (<25 cm in height) to have the same yearly growth (~9-11 cm/yr) as taller, presumably older seedlings (<150 cm). This resulted in a 100-150 cm tall seedling in deer treatments needing over two years worth of growth to equal the yearly growth of a seedling protected from deer. This growth differential increased as the size of the seedling increased until it reached approximately 2 m in height; above which deer could no longer browse the terminal bud.

During the study, vegetation nitrogen content tracked treatment induced shifts in vegetation mass, as N concentrations were not altered by my vegetation manipulations or by deer. Although forb N content did not differ in 2004, rank orders of vegetation manipulation treatment effects (Herbicide + Scarified < Herbicide< Selective< Controls) indicated that deer might have trended to utilizing forbs in more open areas to a greater extent (easier to see) than in areas dominated by sedge (controls).

I expected to find, but did not, that both deer and vegetation manipulation treatments altered levels of extractable N and/or N- mineralization rates, as others have found both can change due to shifting vegetation conditions induced by ungulate browsers (Pastor et al., 1993 & 1998,and McInnes et al., 1992). I may not have witnessed this shift because of the continued dominance of overstory litter inputs into the system (85% of the total litter inputs in control area was from overstory trees).

After four years it was evident that vegetation growing in my study areas experienced seasonal periods of intense climate induced stress. In three of the four growing seasons I observed soil moisture declines while a decline in growing season rainfall was recorded at a local NOAA weather station (Spalding MI). Two of the four growing seasons had droughts that were below the 50-year average. Although the main study showed no soil moisture differences among vegetation manipulation or Deer treatments perhaps because of larger variation and smaller sample sizes,

In general, Although the pressures of sedge on seedling growth has the potential to be a significant driver of succession, this can only occur if/when deer numbers decline, as deer are truly the key drivers of sugar maple regeneration in these northern hardwood system (Waller and Alverson 1997).

Management Implications

If deer populations stay at current levels, the restocking of these highly managed stands should be a concern to managers. As deer halt regeneration from below and trees that are above the reach of deer continue to grow into higher height classes, significant losses of intermediate forest canopy layers will continue and calls into question the long-term sustainability of these managed systems. The fact that deer are eliminating ironwood, a species many consider to be of lower preference to deer, highlights the pressure that the forested systems are under and the suboptimal forage that deer are having to ingest to survive.

If deer densities are lowered, removing sedge while opening the canopy will result in greater seedling growth which reduces the time that deer densities will need to remain lower. Using Figure 2.9 to give us a rough approximation of a sugar maple's potential growth under average light levels (6-11 % open sky). Here a seedling could potentially reach 150+ cm in 7-8 years, if as this data shows, a seedling grows more per year as it grows in stature. Conservatively, managers should use a 10-year window to allow for unforeseen events (droughts, insect defoliations, etc).

The near complete removal of sedge two years after the vegetation manipulation treatments was promising from a management standpoint, as was the 50-55% lower sedge mass found after four years. Unfortunately, the near complete loss of seedlings and recruit seedlings >25 cm, which were also susceptible to the two mid-summer herbicide treatments (herbicide and herbicide + scarification), was a concern. Given the four year "window" of reduced sedge densities achieved with the vegetation manipulation treatments, the periodic mast seeding events common to northern hardwood tree species (Houle 1999), and the potential for moderate to severe growing season drought events, the loss of previously established desired tree seedling individuals should be minimized.

Although I found severe negative deer effects on ironwood growth, this species is poised to dominate the next forest sapling stage on these sites if/when deer numbers decline. Because little is known if high deer densities can be overwhelmed by spraying large areas of competing vegetation, it is currently an economically unwise decision to proceed with spraying before there is an immediate and clear determination on the part of resource managers to reduce the deer herd in parts of Michigan. Further work is needed in identifying methods of spraying which effectively controls sedge while leaving tree seedlings and forbs intact.

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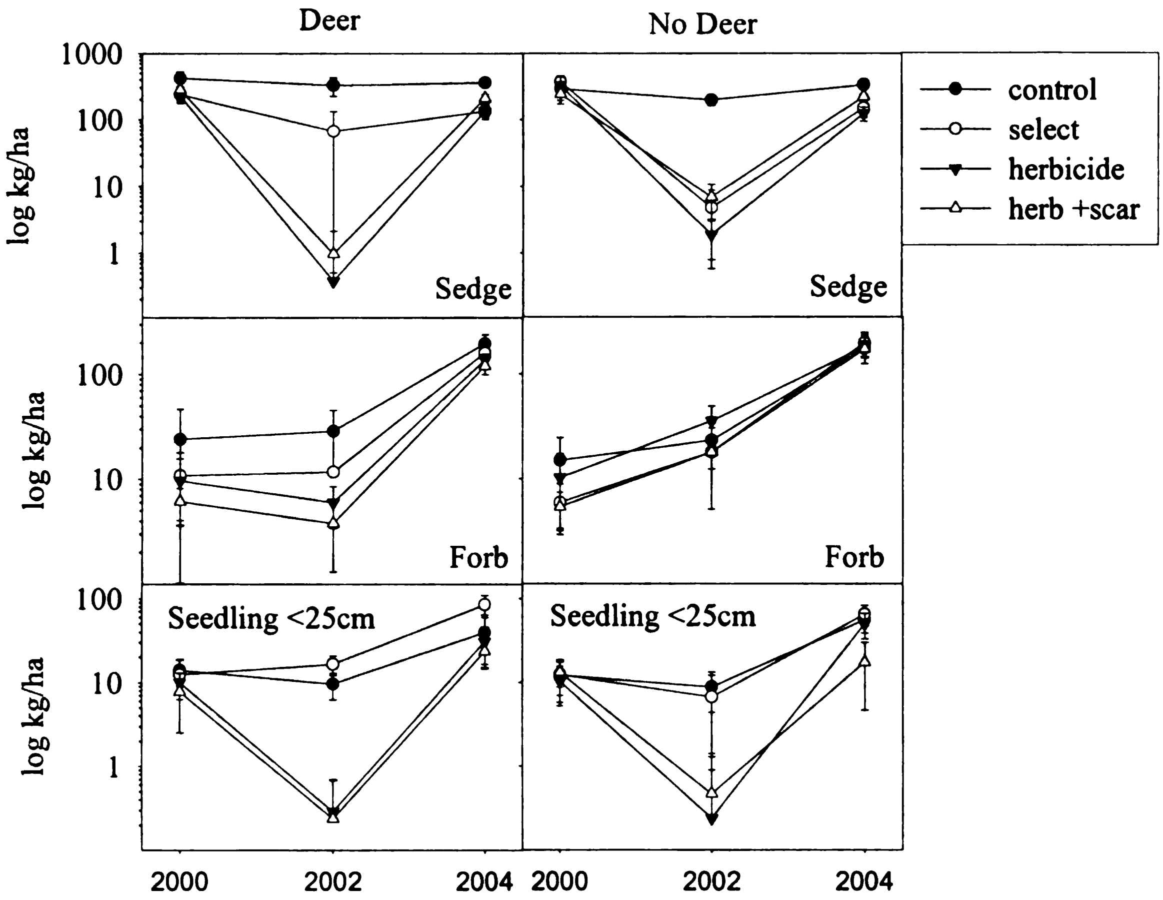

Figure 2.1. Harvested Sedge (A&B), Forb (C&D), and Seedling<25cm(E&F) biomass across sampling years. Treatments nested within Deer and No Deer areas. ± 1 standard error.

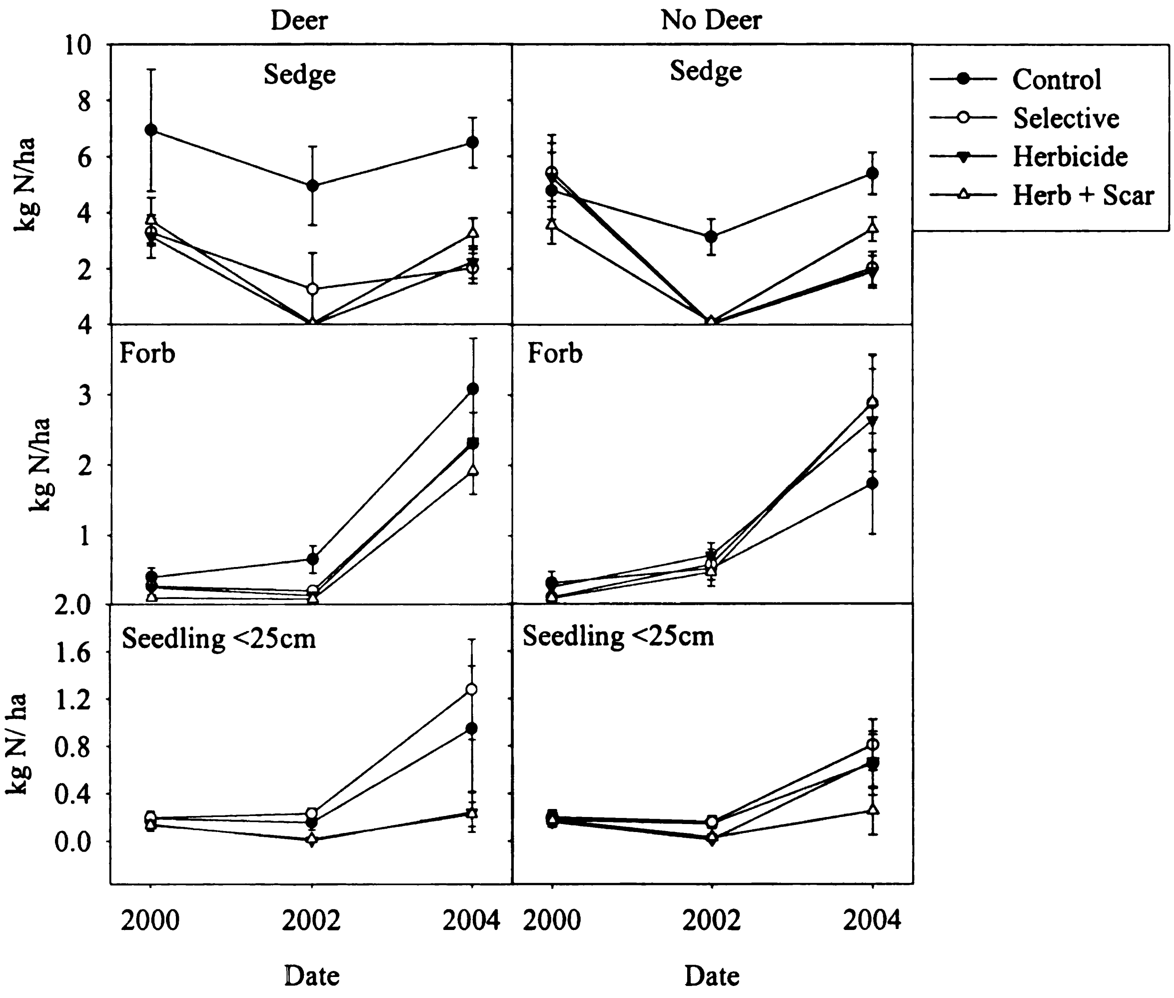

Figure 2.2. Harvested Sedge (A&B), Forb (C&D), and Seedling<25cm(E&F), N content across sampling years. Treatments nested within Deer and No Deer areas. ± 1 standard error.

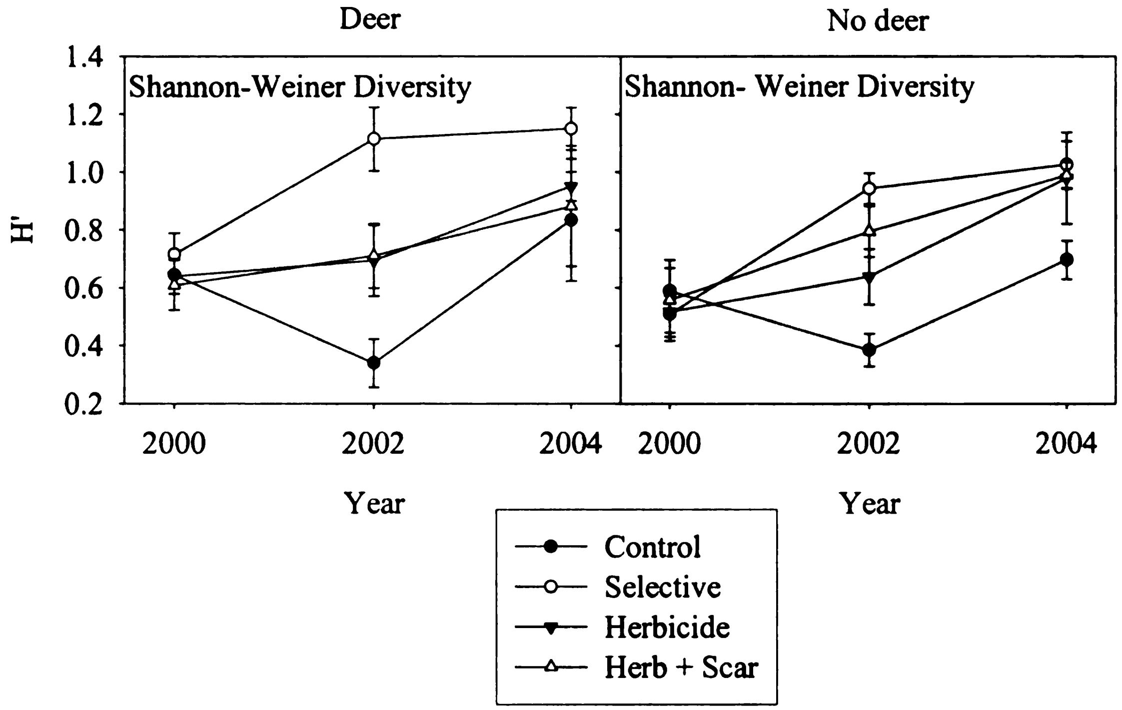

Figure 2.3. Shannon-Weiner Diversity across sampling years by Deer/ No Deer areas with nested treatments. ± 1 standard error.

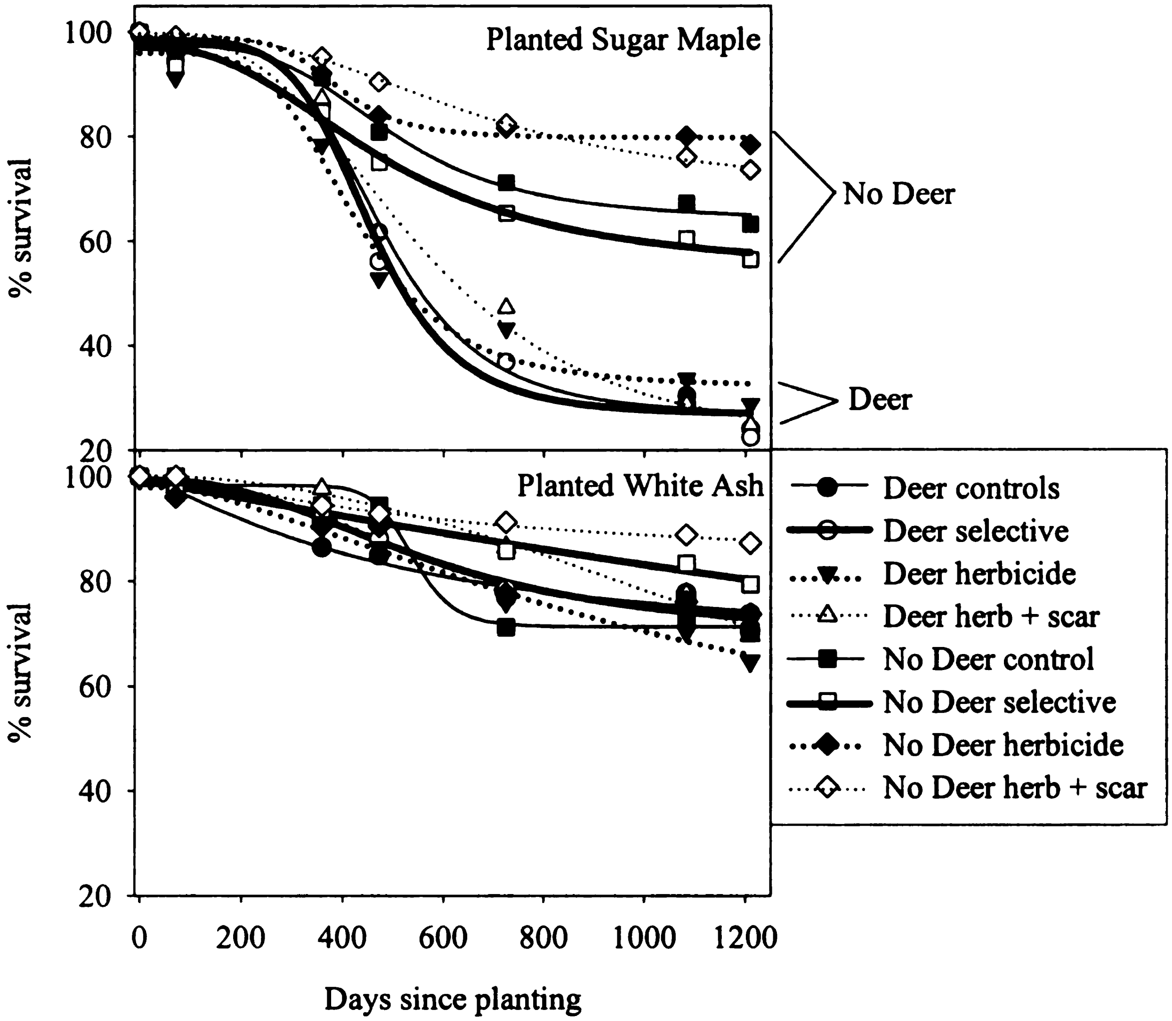

Figure 2.4. Planted sugar maple (4A) and white ash (4B) seedling survival after 1210 days by Deer/No Deer[nested treatments].

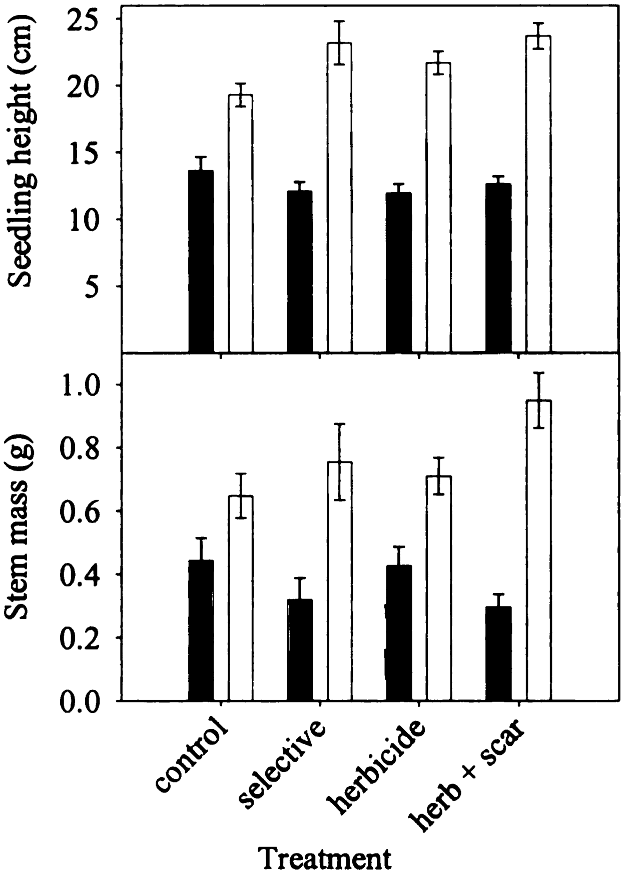

Figure 2.5. Planted sugar maple seedling growth (5A) and stem mass (5B) by treatment and Deer (shaded bars) / No deer (open bars). ± 1 standard error.

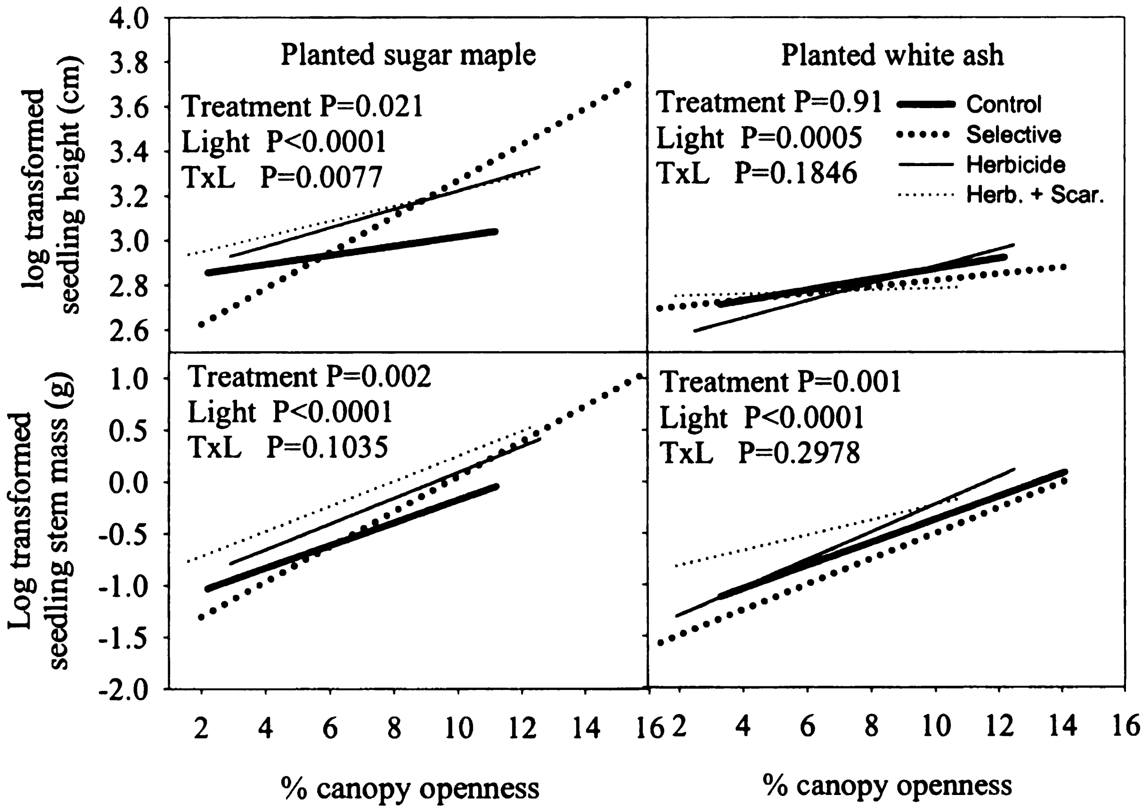

Figure 2.6. Planted sugar maple seedling height (6A) & stem mass (6B), and White ash seedling height (6C) & stem mass (6D) by treatment across a gradient of canopy openness in areas protected from deer.

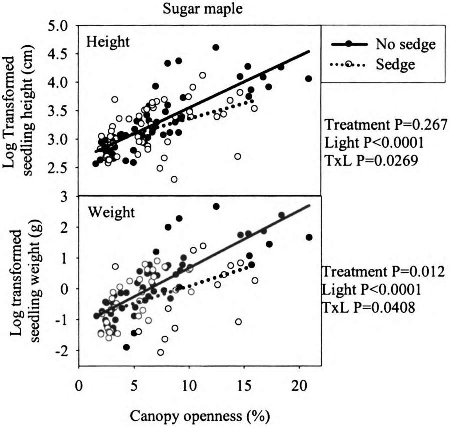

Figure 2.7. Naturally established sugar maple seedling height and dry mass across a gradient of canopy openness in areas with vegetation and without.

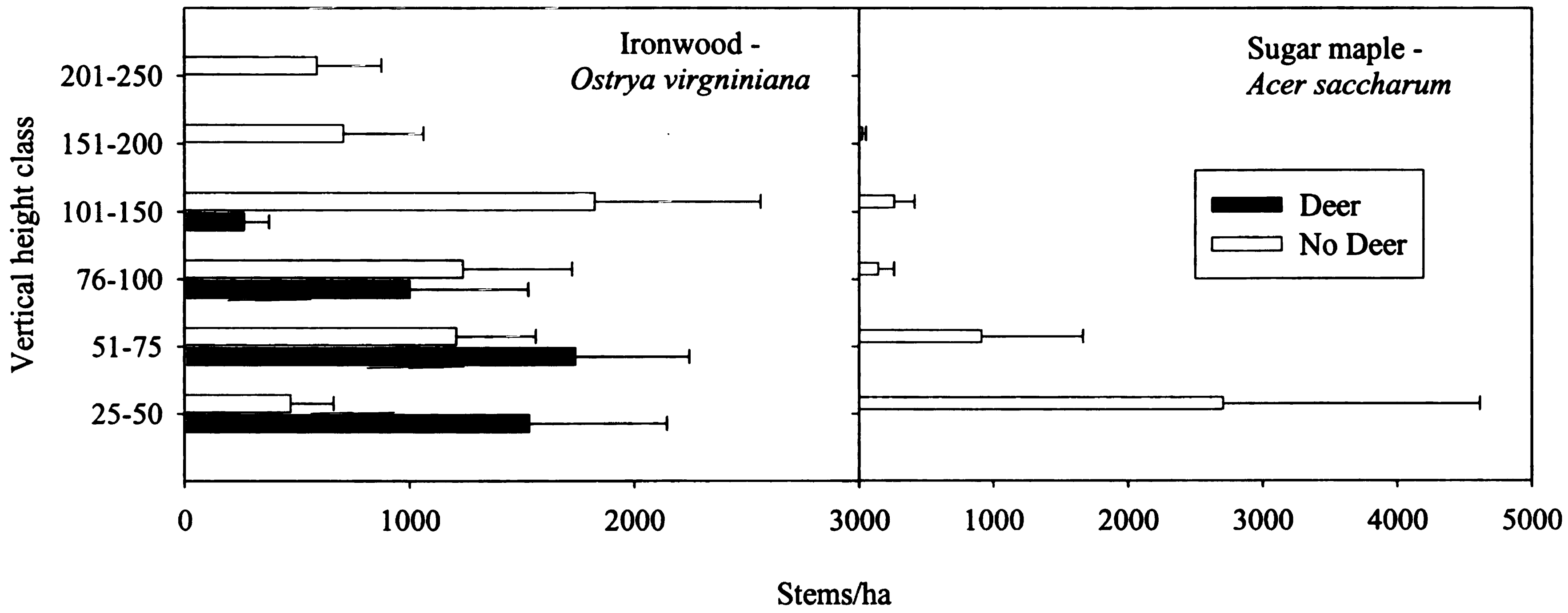

Figure 2.8. *Ostrya virginiana* and *Acer saccharum* stem densities by height class in Deer and No Deer treatments. ± 1 standard error

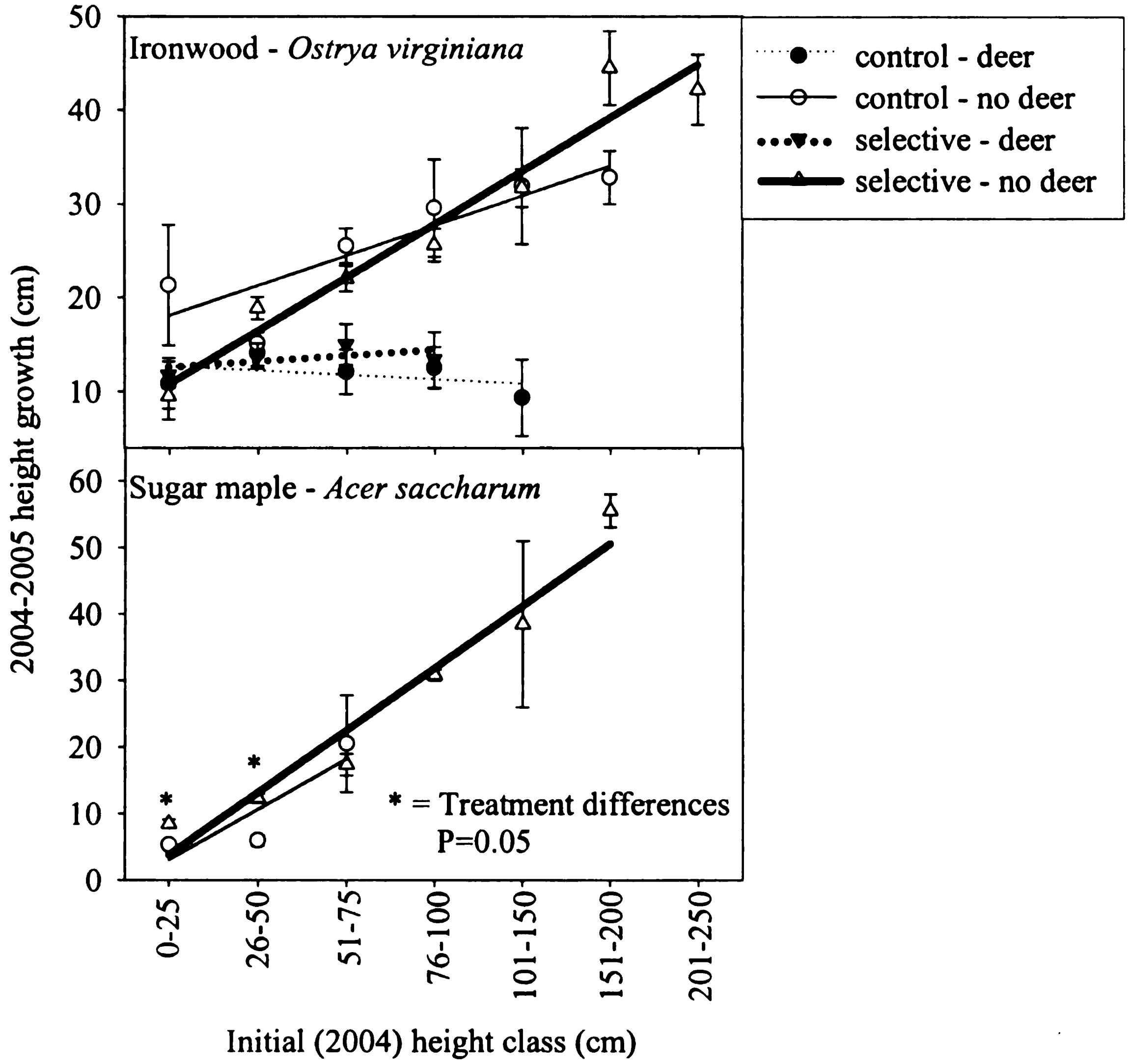

Figure 2.9. 2004 – 2005 *Ostrya virginiana* and *Acer saccharum* height growth by Deer/No Deer and Nested treatments control & selective) separated by initial height class. ± 1 standard error.

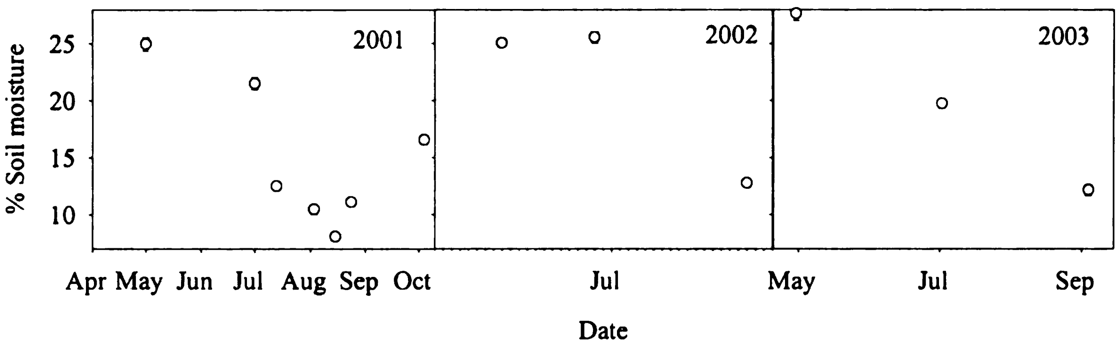

Figure 2.10. % soil moisture over the three growing seasons (2001-2003).

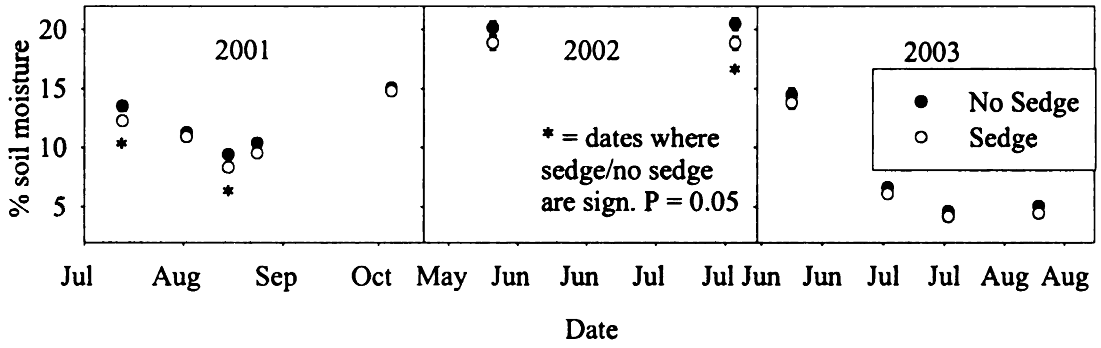

Figure 2.11. % soil moisture from areas with and without vegetation surrounding two year old naturally established sugar maple seedlings.

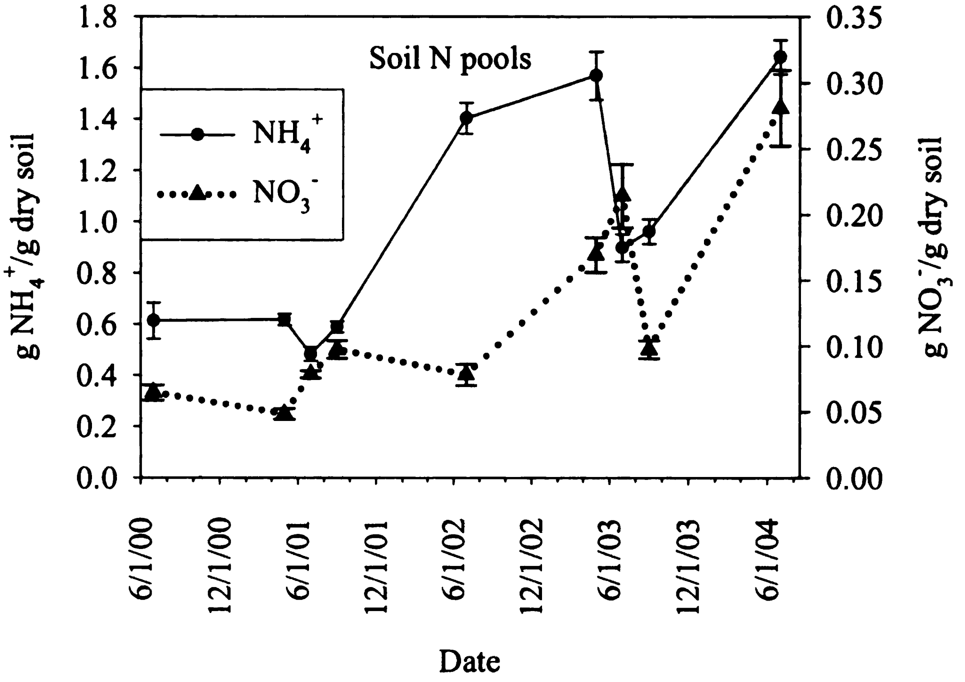

Figure 2.12. Extractable NH_4^+-N and NO_3^- -N collected from 9 measurement points throughout the study. ± 1 standard error.

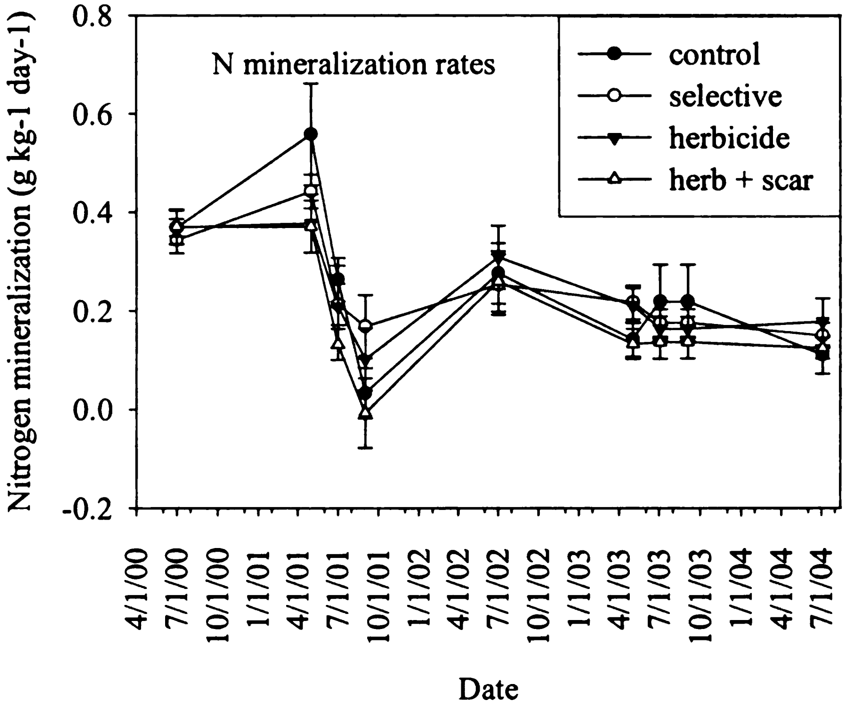

Figure 2.13. N-mineralization rates by treatment from 2000-2004. ± 1 standard error.

Table 2.1. Results of a standard least squares mixed model for the effects of Deer/No Deer, and Deer/No Deer[nested treatments] on sedge (A), forb (B), and seedling (C) biomass, and Shannon-Weiner diversity (D) by years (2000,2002,2004).

Vegetation biomass	ANOVA Effects	2000	2002	2004
A- Sedge	Deer/No Deer	P=0.6706	P=0.8244	P=0.3151
	Deer/No Deer [Veg. manip]	P=0.4569	**P=0.0003**	P=0.0705
B- Forb	Deer/No Deer	P=0.4036	**P=0.0121**	P=0.3297
	Deer/No Deer [Veg. manip]	P=0.3256	P=0.1085	P=0.8801
C- Seedling	Deer/No Deer	P=0.7027	P=0.6398	P=0.4227
	Deer/No Deer [Veg. manip]	P=0.9465	**P<0.0001**	P=0.0584
D- Shannon-Weiner	Deer/No Deer	P=0.0793	P=0.7207	P=0.6041
Diversity (H')	Deer/No Deer [Veg. manip]	P=0.9614	**P<0.0001**	P=0.0987

Table 2.2. Results of a standard least squares mixed model for the effects of Deer/No Deer, and Deer/No Deer[nested treatments] on sedge (A), forb (B), and seedling (C) N content across years (2000,2002,2004) by Deer/No Deer, and Deer/No Deer[nested treatments].

Vegetation N Content	Anova Effects	2000	2002	2004
A- Sedge	Deer/No Deer	P=0.5642	P=0.1459	P=0.4854
	Deer/No Deer [Veg. manip]	P=0.2686	**P<0.0001**	**P<0.0001**
B- Forb	Deer/No Deer	P=0.2377	**P=0.0070**	P=0.7366
	Deer/No Deer [Veg. manip]	P=0.1476	P=0.1529	P=0.5701
C- Seedling	Deer/No Deer	P=0.6945	P=0.5687	P=0.7149
	Deer/No Deer [Veg. manip]	P=0.9596	**P=0.0002**	P=0.1152

Table 2.3. Chi Square results for planted sugar maple and white ash seedling survival (1210 days after planting) by Deer/No Deer, and Deer/No Deer[nested treatments] effects.

	ANOVA Effect	Chi Square	Prob>Chi sq.
Sugar maple	Deer/No Deer	158.9898	**0.0000**
	Deer/No Deer [Veg. manip]	17.5519	**0.0075**
White ash	Deer/No Deer	8.68139	**0.0032**
	Deer/No Deer [Veg. manip]	13.6935	**0.0333**

Table 2.4. Mixed model (Deer/No Deer, and Deer/No Deer[nested treatments] effects) results for Ironwood density (stems/ha) by height class from 34-1m^2 sampling plots/treatment area.

Height class	ANOVA Effect	Sum of Squares	F ratio	Prob>F
25-50cm	Deer/No Deer	5605536	2.462	0.1362
	Deer/No Deer [Veg. manip]	1107266	0.243	0.787
50-75cm	Deer/No Deer	1401384	0.657	0.4294
	Deer/No Deer [Veg. manip]	640138	0.15	0.8618
75-100cm	Deer/No Deer	276816	0.098	0.7587
	Deer/No Deer [Veg. manip]	1003460	0.177	0.8394
100-150cm	Deer/No Deer	12149654	4.051	**0.0613**
	Deer/No Deer [Veg. manip]	2223183	0.371	0.6961
150-200cm	Deer/No Deer	2491350	3.578	**0.0768**
	Deer/No Deer [Veg. manip]	311419	0.224	0.8021
200-300cm	Deer/No Deer	1730104	3.738	**0.0711**
	Deer/No Deer [Veg. manip]	34602	0.037	0.9634

Table 2.5. Mixed model (Deer/No Deer, and Deer/No Deer[nested treatments] effects) results for ironwood growth (2004-2005) by height class from 34-1m^2 sampling plots/treatment area.

IW Initial height class	ANOVA Effect	Sum of Squares	F ratio	Prob>F
0-25cm	Deer/No Deer	0.066957	0.2678	0.6119
	Deer/No Deer [Veg. manip]	0.9892297	0.7912	0.5713
25-50cm	Deer/No Deer	2.0433812	5.2696	**0.0237**
	Deer/No Deer [Veg. manip]	1.0138625	0.6537	0.6256
51-75cm	Deer/No Deer	11.590785	29.4843	**<0.0001**
	Deer/No Deer [Veg. manip]	1.011144	1.2861	0.2809
76-100cm	Deer/No Deer	6.601605	21.1904	**<0.0001**
	Deer/No Deer [Veg. manip]	0.0074903	0.012	0.9881
101-150cm	Deer/No Deer	5.7453133	26.4655	**<0.0001**
	Deer/No Deer [Veg. manip]	0.0925699	0.4264	0.5179
151-200cm	Deer/No Deer			na
	Deer/No Deer [Veg. manip]			na
201-300cm	Deer/No Deer			na
	Deer/No Deer [Veg. manip]			na

Table 2.6. Results of a standard least squares mixed model for the effects of Deer/No Deer, and Deer/No Deer[nested treatments] on gravimetric soil moisture by sampling date.

Date	ANOVA Effect	Sum of Squares	F ratio	Prob>F
July 13 2000	Deer/No Deer	11.079983	0.5178	0.477
	Deer/No Deer [Veg. manip]	86.519846	0.6739	0.6715
May 1 2001	Deer/No Deer	0.234115	0.0159	0.9003
	Deer/No Deer [Veg. manip]	46.728291	0.5301	0.7812
July 1 2001	Deer/No Deer	4.180169	0.396	0.5336
	Deer/No Deer [Veg. manip]	85.971097	1.3573	0.2616
July 13 2001	Deer/No Deer	4.777724	0.7208	0.4022
	Deer/No Deer [Veg. manip]	23.353471	0.5872	0.7379
Aug 3 2001	Deer/No Deer	0.913556	0.1405	0.7103
	Deer/No Deer [Veg. manip]	30.125009	0.7719	0.5977
Aug 15 2001	Deer/No Deer	6.218704	2.2825	0.1407
	Deer/No Deer [Veg. manip]	15.48526	0.9473	0.4757
Aug 24 2001	Deer/No Deer	0.356394	0.0689	0.7947
	Deer/No Deer [Veg. manip]	23.4791	0.756	0.6095
Oct 4 2001	Deer/No Deer	0.646442	0.096	0.7587
	Deer/No Deer [Veg. manip]	10.176175	0.2518	0.955
June 18 2002	Deer/No Deer	14.35204	4.1912	**0.0489**
	Deer/No Deer [Veg. manip]	20.00516	0.9737	0.4588
June 29 2002	Deer/No Deer	0.009661	0.001	0.9754
	Deer/No Deer [Veg. manip]	32.859523	0.5492	0.7668
July 17 2002	Deer/No Deer	14.508202	3.0634	0.0897
	Deer/No Deer [Veg. manip]	18.472395	0.6501	0.6897
April 30 2003	Deer/No Deer	0.02025	0.0013	0.9718
	Deer/No Deer [Veg. manip]	31.422492	0.328	0.9173
July 2 2003	Deer/No Deer	1.602817	0.2678	0.6083
	Deer/No Deer [Veg. manip]	31.998678	0.8912	0.5129
Sept 4 2003	Deer/No Deer	1.164153	0.1258	0.7251
	Deer/No Deer [Veg. manip]	22.955757	0.4136	0.8645
June 22 2004	Deer/No Deer	0.068048	0.0042	0.9489
	Deer/No Deer [Veg. manip]	68.031137	0.6961	0.6545

Table 2.7. Results of a standard least squares mixed model for the effects of Treatment, canopy openness, and their interaction on gravimetric soil moisture by sampling date.

Date	ANOVA effect	Sum of Squares	F ratio	Prob>F
July 13 2001	Treatment	0.2709	5.3504	**0.0225**
	% canopy openness	0.2796	5.5228	**0.0205**
	TxCO	0.1750	3.4560	0.0656
Aug 2 2001	Treatment	0.0237	0.2960	0.5875
	% canopy openness	0.0927	1.1583	0.2841
	TxCO	0.0236	0.2952	0.5880
Aug 15 2001	Treatment	0.4352	5.4587	**0.0212**
	% canopy openness	0.5584	7.0042	**0.0093**
	TxCO	0.0107	0.1336	0.7154
Aug 24 2001	Treatment	19.1344	3.2503	0.0740
	% canopy openness	113.0280	19.2000	**<0.0001**
	TxCO	22.3763	3.8000	0.0537
Oct 5 2001	Treatment	1.0217	0.1398	0.7092
	% canopy openness	44.9415	6.1484	**0.0147**
	TxCO	6.3030	0.8623	0.3551
May 29 2002	Treatment	43.2607	1.9669	0.1635
	% canopy openness	111.1630	5.0541	**0.0265**
	TxCO	10.5850	0.4813	0.4892
July 17 2002	Treatment	65.6580	3.6681	0.0579
	% canopy openness	254.2490	14.2039	**0.0003**
	TxCO	2.2125	0.1236	0.7258
June 23 2003	Treatment	0.0470	0.6168	0.4339
	% canopy openness	1.7962	23.5760	**<0.0001**
	TxCO	0.0615	0.8075	0.3707
July 15 2003	Treatment	6.5255	1.7761	0.1853
	% canopy openness	15.7887	4.2973	**0.0404**
	TxCO	6.3237	1.7212	0.1922
July 29 2003	Treatment	5.0340	3.1604	0.0781
	% canopy openness	15.8687	9.9626	**0.0020**
	TxCO	2.7383	1.7191	0.1924
Aug 19 2003	Treatment	0.2403	3.2076	0.0782
	% canopy openness	0.0312	0.4165	0.5211
	TxCO	0.0806	1.0759	0.3036

Table 2.8. Results of a standard least squares mixed model for the effects of Deer/No Deer, and Deer/No Deer[nested treatments] on $NO3^{-}$-N by sampling date.

Date	ANOVA Effect	Sum of Squares	F ratio	Prob>F
Jul-00	Deer/No Deer	0.285688	1.1606	0.2894
	Deer/No Deer [Veg. manip]	0.39012	0.2641	0.9496
May-01	Deer/No Deer	0.00014	0.0005	0.983
	Deer/No Deer [Veg. manip]	0.373826	0.2005	0.9742
Jul-01	Deer/No Deer	0.0352817	0.158	0.6936
	Deer/No Deer [Veg. manip]	0.795346	0.5936	0.733
Sep-01	Deer/No Deer	0.0015077	0.0337	0.8555
	Deer/No Deer [Veg. manip]	1.62414	0.6051	0.7242
Jul-02	Deer/No Deer	0.1149966	0.2728	0.6051
	Deer/No Deer [Veg. manip]	1.37408	0.5433	0.7713
May-03	Deer/No Deer	0.4625708	1.968	0.1703
	Deer/No Deer [Veg. manip]	0.863546	0.6123	0.7187
Jul-03	Deer/No Deer	0.8157605	3.151	0.0857
	Deer/No Deer [Veg. manip]	8.060257	5.189	**0.0009**
Sep-03	Deer/No Deer	0.0199885	0.3484	0.5592
	Deer/No Deer [Veg. manip]	0.13944	0.4051	0.8701
Jul-04	Deer/No Deer	0.003929	0.1073	0.7455
	Deer/No Deer [Veg. manip]	0.084343	0.3837	0.8838

Table 2.9. Results of a standard least squares mixed model for the effects of Deer/No Deer, and Deer/No Deer[nested treatments] on $NH4^+$-N by sampling date.

Date	ANOVA Effect	Sum of Squares	F ratio	Prob>F
Jul-00	Deer/No Deer	0.00011933	0.0488	0.8266
	Deer/No Deer [Veg. manip]	0.02620413	1.786	0.1346
May-01	Deer/No Deer	0.0100711	0.4389	0.5124
	Deer/No Deer [Veg. manip]	0.068348	0.4964	0.8062
Jul-01	Deer/No Deer	0.1310189	1.0922	0.3038
	Deer/No Deer [Veg. manip]	0.78030672	1.0842	0.3927
Sep-01	Deer/No Deer	0.0003377	0.0064	0.9369
	Deer/No Deer [Veg. manip]	0.36849644	1.1575	0.3531
Jul-02	Deer/No Deer	0.0067181	0.0988	0.7553
	Deer/No Deer [Veg. manip]	0.5866698	1.4378	0.2311
May-03	Deer/No Deer	0.05889284	0.4038	0.5297
	Deer/No Deer [Veg. manip]	0.53568514	0.6121	0.7188
Jul-03	Deer/No Deer	0.6392784	6.9242	**0.0131**
	Deer/No Deer [Veg. manip]	1.4349168	2.5903	**0.0376**
Sep-03	Deer/No Deer	0.16175376	1.6591	0.207
	Deer/No Deer [Veg. manip]	0.48153911	0.8232	0.5605
Jul-04	Deer/No Deer	0.0820113	0.4395	0.5121
	Deer/No Deer [Veg. manip]	1.048238	0.9363	0.4829

Table 2.10. Results of a standard least squares mixed model for the effects of Deer/No Deer, and Deer/No Deer[nested treatments] on N-Mineralization rates by sampling date.

Date	ANOVA Effect	Sum of Squares	F ratio	Prob>F
Jul-00	Deer/No Deer	0.00088	0.1125	0.7395
	Deer/No Deer [Veg. manip]	0.06162	1.3155	0.2788
May-01	Deer/No Deer	0.10747	4.0067	0.0541
	Deer/No Deer [Veg. manip]	0.249227	1.5486	0.1955
Jul-01	Deer/No Deer	0.0000027	0.0002	0.9902
	Deer/No Deer [Veg. manip]	0.146405	1.3828	0.2526
Sep-01	Deer/No Deer	0.000294	0.0069	0.9341
	Deer/No Deer [Veg. manip]	0.237864	0.9349	0.4838
Jul-02	Deer/No Deer	0.020889	0.5715	0.4552
	Deer/No Deer [Veg. manip]	0.155785	0.7104	0.5437
May-03	Deer/No Deer	0.06849	0.1616	0.6904
	Deer/No Deer [Veg. manip]	4.724	1.8575	0.1191
Jul-03	Deer/No Deer	1.186235	1.4757	0.2336
	Deer/No Deer [Veg. manip]	2.22805	0.462	0.8309
Sep-03	Deer/No Deer	0.00197	0.1166	0.7351
	Deer/No Deer [Veg. manip]	0.07134	0.702	0.6501
Jul-04	Deer/No Deer	0.00396	0.3111	0.5809
	Deer/No Deer [Veg. manip]	0.051089	0.669	0.6752

Appendix 2.1. Stand history and structural attributes for the 5 replicate sites.

Stand structure	Sites				
	1	2	3	4	5
habitat classification	AVO	AVO	AVO	AVO	AVO
stand size (ha)	18.6	31.8	20.8	14.5	38.9
stand established	1934	1930	1924	1934	1934
cut year	1972	1975			
cut year	1987	1985	1977	1970	1974
last cut year	1995	1995	1998	1995	1997
Total BA (m^2/ha)	24.68	21.81	23.19	21.81	18.82
SM	6.03	10.90	10.04	12.34	13.77
WA	4.88	3.16	1.43	2.87	0.86
BW	4.59	7.75	9.47	6.03	2.87
Hick	8.32	0.00	0.00	0.00	1.43
2001 Light (%)	8.27 (5.6-11.14)	7.74 (5.74-10)	4.27 (2.34-7.3)	6.12 (3.95-7.26)	6.92 (4.88-9.8)
2003 Light (%)	5.7 (1.1-13.5)	5.73 (1.4-11.9)	3.23 (0.8-7.7)	3.87 (1.2-8.3)	4.75 (0.6-13.0)
2002 Litterfall (kg/ha)	3221	3367	3090	3186	2805
2003 Litterfall (kg/ha)	2816	2993	3620	3366	3725
2004 Litterfall (kg/ha)	3404	3233	3777	3556	3471
2000 SM seed rain/ha	10000	0	0	3333	11667
2001 SM seed rain/ha	0	0	0	1666	1667
2002 SM seed rain/ha	263499	880897	1686667	2439000	3596417
2003 SM seed rain/ha	1111	2222	0	555	1111

Appendix 2.2. Soil depth, Horizon Munsell color description, Soil texture (sand, silt, clay, fine clay) by depth, Soil pH, and soil Bulk density measurements by replicate site.

	Site				
Landform	1	2	3	4	5
Horizon depth (cm)					
Oi	+6 ~ +3	+5 ~ +2	+4 ~ +2	+3 ~ +1	+6 ~ +2
Oe	+3 ~ +1				
Oa	+1 ~ 0	+2 ~ 0	+2 ~ 0	+1 ~ 0	+2 ~ 0
A	0 ~ -4	0 ~ -4	0 ~ -2.5	0 ~ -3	0 ~ -2
E	-4 ~ -7	-4 ~ -6	-2.5 ~ -7.5	-3 ~ -7	-2 ~ -6.5
B	-7 ~ -32	-6 ~ -31	-7.5 ~ -41.5	-7 ~ -34	-6.5 ~ -24
BC	-32	-31	-41.5	-34	-24
Horizon color					
A	10YR3/2	10YR3/1	2.5Y2.5/1	10YR3/1	10YR3/1
E	7.5YR5/4	7.5YR4/1	10YR5/2	7.5YR4/1	7.5YR4/1
B	7.5YR4/4	7.5YR5/4	7.5YR5/4	7.5YR5/4	10YR5/4
BC	5YR3/4	5YR3/4	5YR3/4	5/YRY3/4	5YR3/4
Texture (%) 0-20cm					
Sand	42.56	42.51	45.56	42.71	42.76
Silt	49.33	49.40	46.34	49.16	51.13
Course Clay	5.07	6.07	6.08	6.10	5.09
Fine Clay	3.04	2.02	2.03	2.03	1.02
20-40cm					
Sand	39.41	40.29	40.43	38.35	38.33
Silt	47.45	49.64	49.46	51.55	52.59
Clay	7.07	4.03	5.05	6.06	5.04
Fine Clay	6.06	6.04	5.05	4.04	4.04
40-60cm					
Sand	39.39	38.59	40.48	42.57	33.28
Silt	47.48	44.15	46.37	42.22	58.65
Clay	5.05	5.08	6.07	6.08	4.03
Fine Clay	8.08	12.19	7.08	9.12	4.03
Bulk density	0.79	0.82	0.73	0.81	0.61
pH	6.23	7.1	6.86	6.87	6.74

CHAPTER 3

CAN HERBICIDE APPLICATIONS BE TIMED TO CONTROL CAREX PENSYLVANICA LAM. WHILE MINIMIZING IMPACTS TO NON-TARGET VEGETATION IN GREAT LAKES NORTHERN HARDWOOD FORESTS?

Executive summary

Dense *Carex pensylvanica* Lam. (upland sedge) mats can be found in northern temperate forests with higher deer densities and may strongly compete with regenerating tree seedlings for resources. Because sedge is photosynthetically active in the autumn when much of the deciduous vegetation is dormant, I hypothesized that sedge could be controlled with a late fall herbicide application with minimal impact on other vegetation. Here, I report the results of a glyphosate application timing (November 1, July 15, control) experiment conducted in a managed northern hardwood understory. Two years after treatment, November 1 herbicide application reduced sedge biomass 92%, maintained herb biomass, and increased understory plant species richness. November 1 treatment also had the twice the sugar maple seedling germination, establishment, and survival vs. control areas while seedling survival in July 15 treatments was higher than controls, but still less than November treatments. Canopy openness conditions varied within treatments and mixed statistical models showed that increased openness lead to increased herb and seedling mass across all treatments, and increased sedge mass in the controls. Questions still remain as to the November 1 treatment's effectiveness at establishing seedlings that grow into and through the zone of deer browsing in areas with high deer densities. More work is needed to determine potential for large scale whole

stand level treatments

Introduction

Commercially productive selection-harvested northern hardwood stands in areas of the southern Upper Peninsula of Michigan often have very high sedge (*Carex pensylvanica* Lam.) cover (i.e. > 85% of the total understory herb layer biomass (Chapter 1& 2), and in many of these areas, tree recruitment failure is prevalent (Chapter 1 & 2). High sedge cover may be caused by the combination of a long history of selection harvesting practices (frequent disturbances) and high long-term white-tailed deer (*Odocoileus virginanus*) densities (~ 30 deer/km^2 since the mid 1970's). Sedge may increase in areas with high deer densities as it is not preferentially browsed by deer, possibly due to high foliar silica contents (Prychid et al., 2003), and/or lower foliar N values due to stress induced retranslocation from foliage to roots (Heckathorn and Delucia 1996). Lower foliar N concentrations when faced with elevated ungulate pressures is not the rule as I found similar N concentrations between areas with historically elevated deer browsing pressure and areas with lower browsing pressure (chapter 1 & 2). Furthermore, sedge's intercalary meristem growth from belowground rhizomes, and not from a permanent aboveground stem with nutrient rich buds like tree seedlings, protects the plants active growth point from deer. The protection is primarily through avoidance, as the majority of sedge mass is inaccessible during the winter months when deer are forced, due to snow cover, to consume forage of poorer quality, often switching their diets to consume essentially only woody aboveground browse. Sedge, once established, may maintain dominance for long periods of time, even if deer are removed, perhaps because it competitively excludes other plants from colonizing (e.g.

sequesters all growing space clonally) or it creates lethal conditions, which increase mortality of colonizing plants (i.e. decreases soil water, nitrogen, light etc.).

The use of herbicides to reduce competition with conifer crop trees is well understood and is a common operational practice (Cogliastro et al., 1990, Bell et al., 1997, Vreeland et al., 1998). In contrast, using herbicides to control competitors of deciduous northern hardwood tree seedlings is less studied and applied (Horsley 2001, but see Horsley 1981, and Willoughby et al., 2006). Using a non-selective foliar-contact herbicide such as glyphosate to control competitors of broad-leaved species could have some advantages, as it is inexpensive and highly effective. However, its obvious disadvantage is that native, non-competitive plants and desired tree seedlings are equally sensitive to the herbicide, thus potentially making broadcast applications difficult. A possible solution is to apply non-selective herbicide when target vegetation is actively growing (and thus herbicide sensitive) and non-target vegetation is dormant and unsusceptible. In mid to late fall (late October- early November), young tree seedlings and forbs are dormant while sedge leaves are green and presumably active. This late fall period might provide a window to target sedge with a reduced risk of secondary damage to the desired tree seedlings and forbs. If high sedge cover is partially responsible for inhibiting the reestablishment of tree seedlings and forbs, then it seems logical that reducing sedge covers with management interventions such as timed herbicide applications would increase tree, shrub, and forb establishment.

In this study, I compared the effects of a summer spray (July 15), a late fall spray (November 1) and an untreated control on sedge cover and mass, tree seedling germination, growth and survival, as well as understory species richness and diversity of non-target flora. Because light likely varied within and among treatments potentially affecting covers and mass of understory flora I measured light availability at the forest floor could by using canopy openness (proxy for light) as a covariate in the analysis of treatment effects.

Methods

Site characteristics

This field experiment is located in a 195 ha managed northern hardwood stand on International Paper (IP) lands in Menominee County, Michigan. The stand is dominated by sugar maple (*Acer saccharum* Marsh) with white ash (*Fraxinus americana* L.), basswood (*Tilia americana* L.), black cherry (*Prunus serotina* Ehrh.), American elm (*Alnus americana* L.), and hop hornbeam (*Ostrya virginiana* Mill.) as minor components. The stand is on a highly productive drumlin formed from dolomite and limestone parent material that is generally within 9.1 – 15.2 m of the surface and is classified as being part of the Northern Lake Michigan (Hermansville) Till Plain. Soils are moderately to well-drained spodisols and alfisols (Albert 1995). The growing season averages 140 days and 355 mm of rain falls from May through August (48-year average, NOAA-Spalding MI). Like most managed northern hardwood forests in the region, the stand has been selectively harvested at 8-12 year intervals since the 1960s, typically to a residual basal area of 17-18.3 m^2/ha. The most recent selection harvest conducted three years prior to the beginning of my study significantly reduced residual basal area to levels lower than past harvests on the site. Residual basal area on the site was 11.5-13.8 m^2/ha in 2002 when the project began.

Experimental design

In June 2002 I located three sites within the same stand along a productive drumlin and delineated three, 0.2 ha treatment areas per site centered under large harvested canopy gaps. Each 0.2 ha area was randomly assigned to one of three replicates of the three vegetation manipulation treatments: 1) July 15 Glyphosate application (4.7 liters/ha), 2) November 1 Glyphosate application (4.7 liters/ha), and 3) a control (no herbicide). See experimental overview diagram (Appendix Figure 3.1.), which shows layout of treatments, vegetation measurements (explained below) and seed trap positioning (explained below) for one of the three replicates used in the study.

Vegetation Measurements

Within each 0.2 ha treatment area I established a grid (buffered by 8 m to minimize edge effects including herbicide drift), and marked 24-1.5 m x 1.5 m permanent vegetation sample plots. In these sample plots I, along with another observer, measured vegetation percent cover with ocular estimates and counted tree seedlings <0.25m tall in mid July of 2002 just prior to the July herbicide treatment, and again in mid July of 2003 and 2004. Spring ephemeral herb percent cover estimates were taken in May of 2003 and 2004. Given sedge's dominance in the understory, which increases the potential likelihood of biasing ocular estimates of vegetation growing within the sedge, two observers simultaneously estimated cover and estimates were averaged. Tree seedlings were censused for survival on a monthly basis from May to October of 2003, in late May and late September of 2004 and 2005, and early June of 2006.

In 2004 I located a 1 m x 1 m sampling area directly to the north and west of the non-destructive sample plots. In these plots I non-destructively estimated percent cover of all forest floor vegetation, counted tree seedling stem density, and then destructively sampled and pooled vegetation from the core area (0.25 m^2) into sedge, forbs, and tree seedlings < 0.25 m tall categories. For seedlings > 25 cm I placed biomass into vertical strata (e.g. 0-25 cm tall, 25-50 cm, etc.). Vegetation was transported to Michigan State University's Tree Research Center, dried for 72 hours at 70°C, and weighed.

Tree seed fall, and canopy openness

I evenly dispersed 12-0.5 m x 0.5 m seed traps between the vegetation sampling areas, elevated to 1 m above the ground (to reduce seed predation by rodents), in each of the 0.2 ha treatment areas to measure yearly seed fall. Traps were collected after leaf drop (prior to snow fall) and seed was sorted in the lab by species, counted for total seed, and sugar maple seed viability was evaluated by opening a subset of samaras and observing if the seed was filled or empty and if the embryo was alive (bright green and soft) or dead (brown and dessicated).

Canopy openness, an estimate of light availability, was measured in mid July 2003 at 1 m above each non-destructive sample plot with a dual LAI 2000 (LiCor Inc., Lincoln NE) setup. The setup and calibration was exactly the same as in chapter 2 and the open field instrument was placed in an open field < 1.6 km from where understory canopy measurements were taken.

Analysis:

The study was originally designed to have three replicate sites with each site having three treatment areas (control, November 1, and July 15), but due to vandalism I was forced to abandon one of the three sites, leaving the study with two replicates of each treatment. In each replicate I averaged data from vegetation plots (n=24) and seed traps (n=12). I used JMP (5.1) statistical software (SAS institute, Cary, NC, USA) for all statistical analyses. ANOVA was used to examine the effects of herbicide treatments on sedge, seedling, and forb biomass, the density of viable sugar maple seed fall, and sugar maple germinants/ha. For significant ($P < 0.05$) ANOVA effects, Tukey Kramer HSD was used to test for significant differences among treatments.

Within treatment replicates, there was large variation in overstory canopy openness, which could affect forest floor vegetation characteristics. Thus, in addition to ANOVA analyses of treatment means, I analyzed vegetation measurements using sample plots as experimental units ($n = 48$, 24/ replicate x 2 replicates) with mixed models that included treatment as a nominal variable, canopy openness as a continuous variable, and their interaction.

I examined species richness for vegetation < 0.25 m tall by bootstrapping data to obtain multiple estimates of the number of unique species for each 2.25 m^2 plot area gradation. By fitting the mean of these bootstrap generated estimates, I was able to develop smoothed species area curves for each treatment. To facilitate testing of species/area curves, I used ANOVA and tested only the largest sampling area unit (27 m^2). The effect of herbicide application on seedling survival was analyzed with Cox's proportional hazards modeling (Cox 1972).

Results

In control plots, sedge dominated forest floor biomass, constituting over 85% of the total. Two years after application, sedge mass was 98% lower in July 15 herbicide areas and 92% lower in November 1 herbicide areas than in control areas (Table 3.1). Forb mass did not differ among treatments (Table 3.1), although there was a weak trend of approximately 30% greater forb mass in both herbicide treatments than in controls. 2002 seed fall, 2003 first year seedling density, and seedling germinant mass were not significantly different among treatments despite large differences in means, perhaps due to low replication (n=2) (Tables 3.1 & 3.2).

In models including both treatment and canopy openness, sedge mass increased with canopy openness in control treatments and was negligible at all light levels in herbicide treatments (Figure 3.1A.). Seedling stem density (only post-treatment germinants), and mass (pre- and post-treatment germinants combined) both treatment and canopy openness was significant, but their interaction was not (Figure 3.1C, D). Seedling stem density and mass decreased with canopy openness and values were greater in November 1 herbicide than in July 15 herbicide and control treatments. Increasing canopy openness increased forb mass while individual treatments did not differ (Figure 3.1B). It is important to note that greater first-year seedling stem densities in the November 1 herbicide treatment was not due to increased seed fall in the autumn of 2002, as control and July 15 treatments had roughly 4 times more viable seed fall than the November 1 treatment. By the start of the third growing season (1099 days), tree seedling survivorship was significantly higher in the November 1 (59%) than the July 15 treatment (44%), and both were greater than the control treatment (31%) (Figure 3.2).

Herbicide treatments affected mid-season (July 15) ground flora species richness measured two years after herbicide treatments. The November 1 treatment had greater species richness than the control treatment, and both November 1 and control treatments had significantly greater species richness than the July 15 treatment (Figure 3.4A). Species richness of spring (late May) censused forbs two years after treatments were nearly identical for both November 1 and control treatments and both had significantly more species than the July 15 treatment (Figure 3.4B). For mid-season species richness, a significant treatment x canopy openness interaction ($P<0.0001$ Adj. $R^2 = 0.40$) indicated that the November 1 treatment responded positively to increased canopy openness (Adj. $R^2 = 0.2921$, $P < 0.0001$), whereas both July 15 and control treatments did not (July 15, $P = 0.78$ & Control $P = 0.96$ respectively). Spring ephemeral herb richness increased with canopy openness in both November and July herbicide treatments, while control area richness did not respond to increasing canopy openness conditions. Dividing mid-season ground flora into "weedy" and "non-weedy" components did not yield any significant treatment effects, but weedy species trended to increase in herbicide treatments (Appendix 3.2.) and increase with canopy openness, but only in the November 1 herbicide treatment (Figure 3.1E).

Overall forest floor layer diversity (Shannon-Weiner) varied by year (Y, $P<0.0001$), treatment, and year X treatment interaction (overall model Adj. $R^2 = 0.409$, $P<0.0001$). Within sampling years (2002, 2003, & 2004), November 1 treatment had higher diversity than either the control or July 15 treatment. Although this order was maintained from 2002-2004, the 2004 treatment effect was not significant (Table 3.3). In mixed models of Shannon-Weiner diversity, treatment effects were significant in 2003 and 2004 and treatment X canopy openness interactions were significant in 2002 and 2004.

Discussion

A single application of a non-selective herbicide (glyphosate) during autumn reduced *Carex pensylvanica* Lam. mass by 92% for at least two years, while having fewer negative effects on non-*Carex* vegetation than a mid-summer herbicide application. Forb mass did not show significant treatment effects but did trend towards increasing in both herbicide treatments relative to controls, possibly as a result of increased availability of rooting space when sedge was killed. Direct herbicide induced mortality of summer and spring active forbs decreased overall species richness levels in the July 15 application areas and those species that were present were more likely to be ruderal or weedy species.

Surprisingly, I found large gains in seedling mass (2.7-fold increase) and densities (2.1-fold increase) in the November 1 treatment but not in the July 15 treatment compared to the controls, despite greater seed fall in the July 15 treatment. The majority of the sugar maple seed fell after the July 15th spray treatment but before the November 1st treatment (personal observation) and was therefore on top of the glyphosate killed sedge in the July 15 treatment, potentially exposing the seed to increased levels of predation and desiccation throughout the fall (DeStevens 1991, and Meiners and Stiles 1997). The vast majority of sugar maple seed fell prior to the November 1 treatment and was then covered with herbicide killed sedge biomass potentially providing better protection from seed predators and from desiccation.

For sugar maple seedlings that established post-treatment, survival rankings were November 1 > July 15 > control treatment and was not likely due to deer herbivory as the incidence of browse damage ranked differently; July 15 > November 1 > control. Instead, lower survival in control areas was likely due to maple's inability to survive drought events(Chapter 4). Levels of drought severity may be increased by the additive effects of sedge moisture withdrawal and use in the understory and the withdrawal and use of water resources by overstory trees .

Greater browsing by deer in herbicide application areas may be due to greater seedling visibility and/or a greater nutritional browse value (e.g. higher leaf nitrogen, lower lignin or silica content) of the seedlings (Anderson et al., 2001) as a result of decreased N competition when sedge populations decline. Interestingly, sedge foliar N concentrations were found to be similar between control and herbicide treatments and overall levels of foliar N were comparable to tree seedling foliage, which also did not change with mid-summer spray or selective sedge removal treatments vs. controls (Chapter 2).

Management Implications

Results suggest that managers, if they wish to control sedge using relatively inexpensive non-selective herbicides (i.e. Glyphosate), should spray at the end of the growing season (late October-early November) and not during the summer months when both advanced tree seedling regeneration and forbs are actively growing.

The greater proportion of seedlings damaged by deer in herbicide treatments vs. control areas may reflect deer being attracted locally to treatment units with higher proportional forb and seedling mass. If true, then it is possible that the browsing patterns I observed are an artifact of the 0.2 ha size of my treatment areas. Increasing the size of the treatment area could overcome this effect, as deer may be more locally dispersed, overwhelming the foraging capacity of the local deer herd and thus reducing browse pressure (Buttrick 1923, Zillgitt 1950).

Managers need to consider other techniques in addition to treating the understory, that will overwhelm a deer's ability to browse all regeneration. This might involve increasing the size and intensity of harvests, along with increasing the harvest interval. Shifting from a single stand harvesting scale to larger landscape oriented practices to reduce deer-preferred edge habitat (Andren and Angelstam 1993) and deer use (browsing) in the core areas (Blymyer and Mosby 1977). Deer have been found to utilize browse primarily within 300m of swamp conifer (cedar) stands in winter months where snow depths range from 20-50cm (Morrison et al., 2002). Lebouton (personal communication of unpublished data) found deer density decreased from 20 to 5 deer/km^2) from lowland conifer stand edge to 800m into northern hardwood stands. A density of 5 deer/km^2 (at 800m from conifer cover) is below the 7 deer/km^2 threshold for timber regeneration suggested by (Hester et al., 2004). As such, forest managers could reduce the acreage of swamp conifer within a buffer zone (300-800m) around northern hardwood stands prior to harvesting the hardwood stand. The reduction in thermal cover and protection from predators, along with increased distance from remaining thermal cover (increased energy expenditures – Moen 1976), and increased snowpack in large cutblocks (decreased food availability) might alter a deer's wintertime deeryard fidelity (Van Deelan 1999). Taken together, this might relax over-winter browsing pressure long enough for seedlings to grow above the reach of deer.

There are downsides to this approach as these lowland conifer stands are highly diverse ecosystems, are preferred by deer for browse leading to regeneration problems, and removal of cedar overstories can reduce water table depths altering revegetation composition and structure. Socially, lowland swamp conifers are viewed by many as the deer herds only chance of surviving Michigan's harsh winters in the northern zones. The state DNR has even placed an emphasis on acquiring strategic blocks of lowland conifers with the sole intent of providing wintertime habitat for deer (MDNR-Deer Range Improvement Program). In the past, during extremely harsh winters managers even would strategically cut small portions of cedar to provide deer with browse.

There are also several factors to be considered before deciding to use widespread herbicide application on forest understories that have failed to regenerate. The first, is the extent of sedge cover and its competitive effect on seedlings on the site in question. This work (Chapters 2 & 4) has shown that sedge can decrease both growth and survival of northern hardwood trees. However, high deer browsing pressure can have such strong direct effects on regeneration that spraying alone would have little effect on seedling recruitment into the sapling class (Chapter 2). Aside from the sedge and deer components, the composition of the advanced tree seedling regeneration in the understory is also important, as economically undesirable tree species may dominate (e.g. *Ostrya virginiana*). Fall spraying may promote these unwanted species, causing further complications to successful establishment of high valued timber species. If species such as ironwood dominate, then a late summer/early fall spray could be used to control both sedge and tree regeneration les desirable for management, but damage to summer active forbs should be expected, while early spring ephemerals should be spared.

Once the extent of sedge is quantified, deer impacts are known, and advanced regeneration has been quantified, the decision to spray becomes an economic one. With the recent advances made in spray delivery systems, such as "boomless" sprayers mounted directly on or pulled behind ATV's or tractors, and the increased availability of generic, lower cost glyphosate, land managers may be able to effectively, and perhaps economically spray entire forest understories. These new spray systems will also extend the spray window, as it is not necessary to wait until overstory trees are leafless as is required if herbicide is delivered with a helicopter or fixed wing aircraft. Finally, although there may be many benefits associated with fall spraying of sedge, caution should be used if its implementation is to work. Stand type, harvesting regime, site differences (productivities) and spatial extent will yield different results. Managers should plan cautiously and perhaps initiate their own trials to test the efficacy of this work in their own stands.

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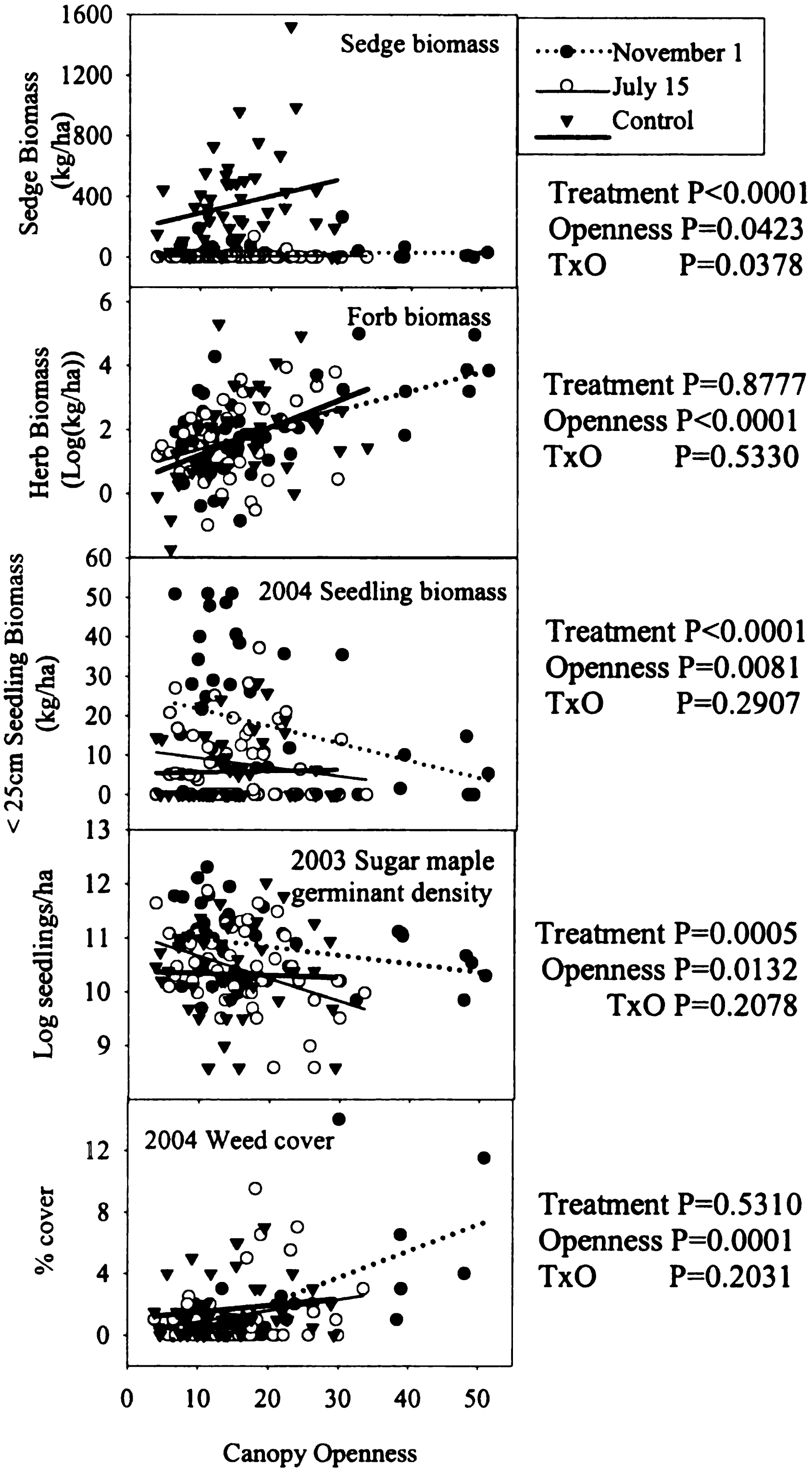


Treatment P<0.0001
Openness P=0.0423
TxO P=0.0378

Treatment P=0.8777
Openness P<0.0001
TxO P=0.5330

Treatment P<0.0001
Openness P=0.0081
TxO P=0.2907

Treatment P=0.0005
Openness P=0.0132
TxO P=0.2078

Treatment P=0.5310
Openness P=0.0001
TxO P=0.2031

Figure 3.1. Sedge biomass (1A), Forb biomass (1B), Seedling biomass (1C), Seedling density (1D), and Weedy % cover (1E) across a % canopy openness gradient by treatment (November 1, July 15 & control).

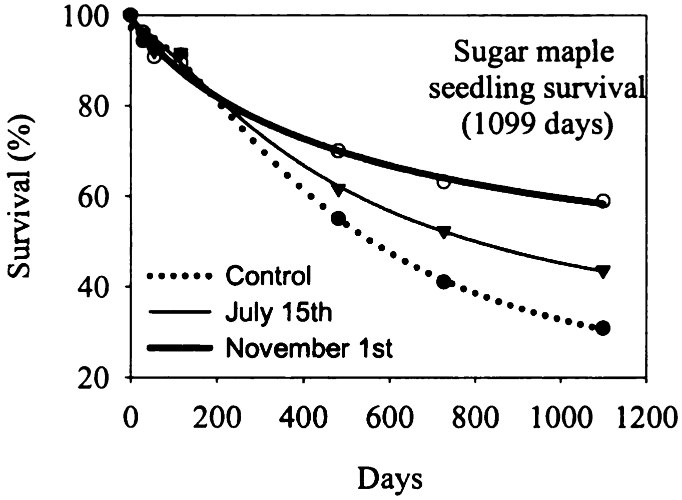


Figure 3.2. Sugar maple seedling survival by treatment (November 1, July 15 & control). (this graph tracks on the survival of seedlings which established following the November and July herbicide applications.)

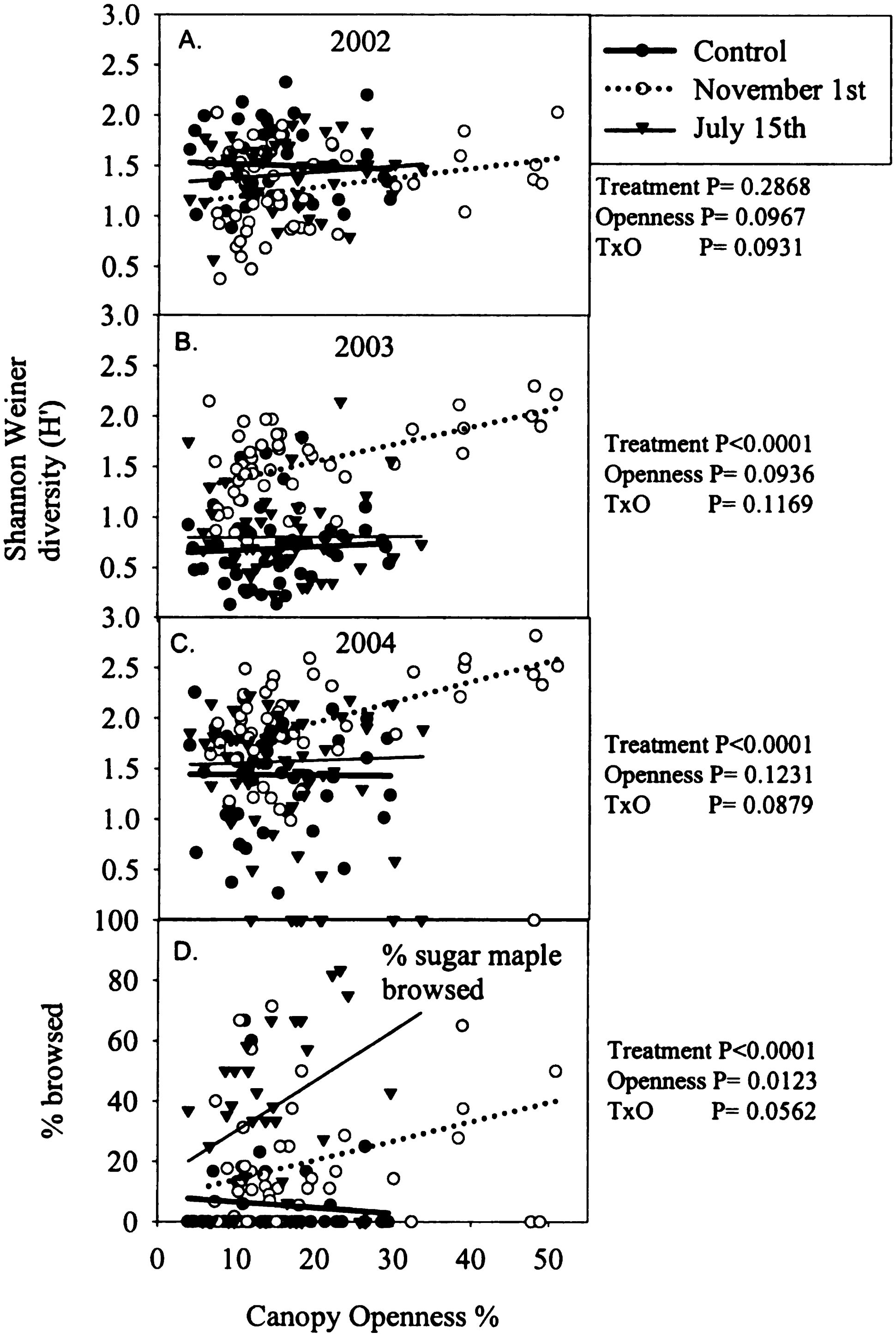


Figure 3.3. 2002, 2003, and 2004 Shannon-Weiner diversity by treatment across a % canopy openness gradient.

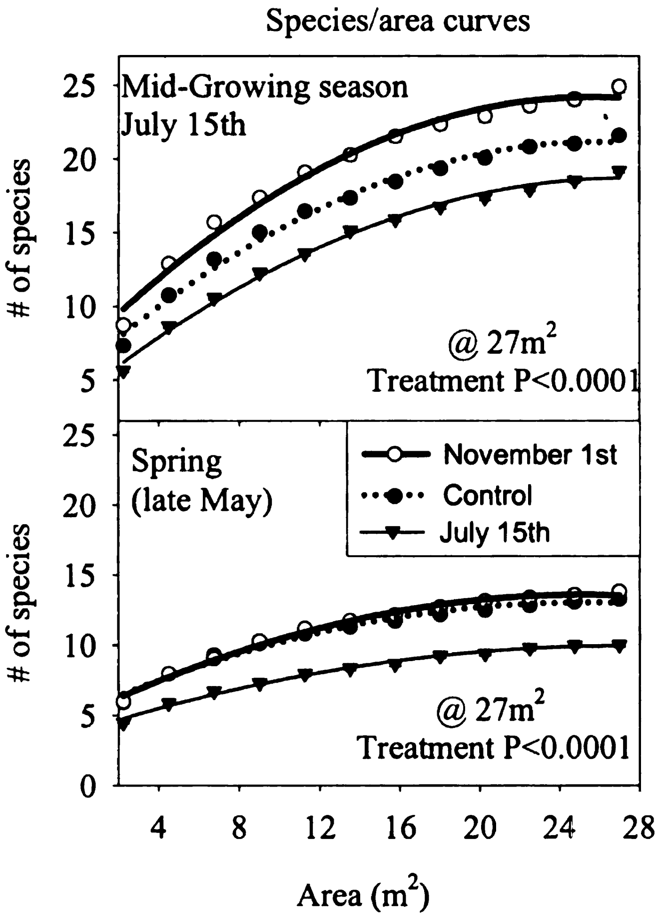


Figure 3.4. Species per unit area sampled by treatment (November 1, July 15 & control) for Mid growing season (top graph) and Spring (bottom graph) census periods.

Table 3.1. Forb, Seedling, and Sedge biomass (kg ha^{-1}) by treatment (Control, November 1, & July 15).

Treatment	forb kg/ha	seedling kg/ha	sedge kg/ha
Control	49.2 ± 13.13 a	8.6 ± 1.54 a	345.2 ± 2.658 a
November 1	64.0 ± 33.07 a	23.0 ± 1.047 a	27.1 ± 10.147 b
July 15	62.3 ± 38.67 a	9.19 ± 5.49 a	5.77 ± 3.327 b

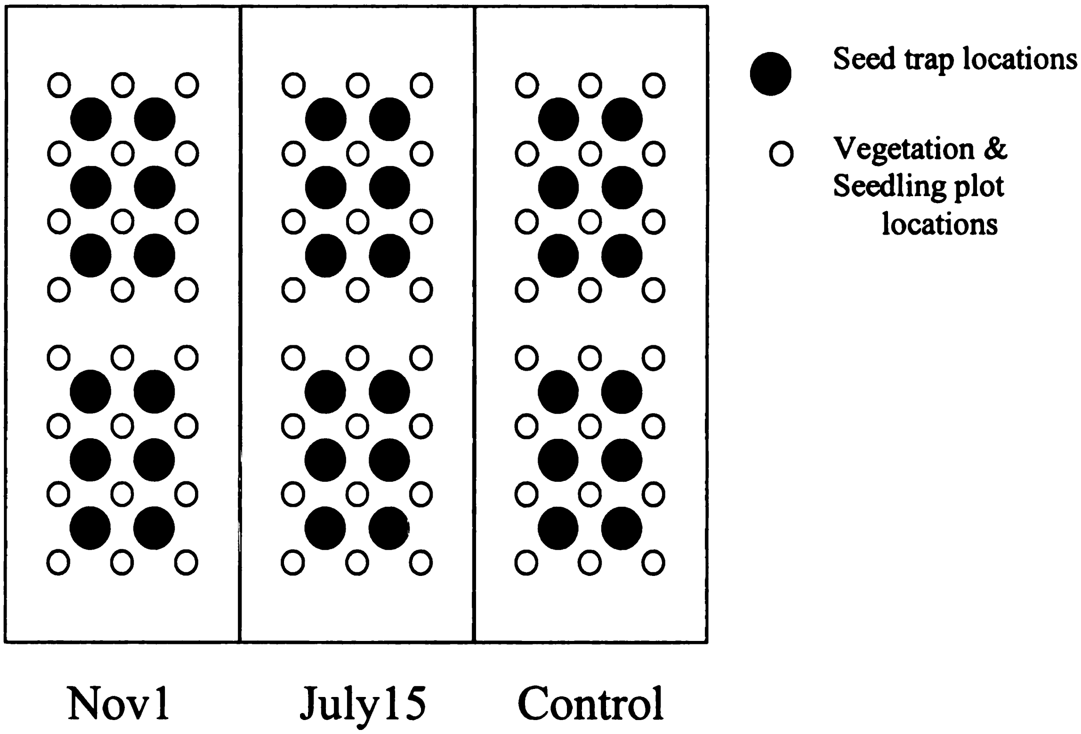
Table 3.2. Viable seed rain/ha, and Sugar maple germinants/ha by treatment (Control, November 1, & July 15).

Treatment	2002 viable seed fall/ha	2003 sugar maple 1st year seedlings/ha
Control	1996205 ± 1587295 a	38958 ± 2292 a
November 1	412435 ± 92564 a	82083 ± 24167 a
July 15	1843333 ± 968333 a	48958 ± 17292 a

Table 3.3. Shannon-Weiner diversity indices for years 2002, 2003, and 2004, and % ruderal and non-ruderal herbaceous cover by treatment (Control, November 1, & July 15). Different letters represent significantly different (P=0.05) means within a column (year).

	Shannon-Weiner Diversity: Mid-July			% herbaceous layer cover	
Treatment	2002	2003	2004	Non-ruderal	Ruderal
Control	1.50 ± 0.02 a	0.69 ± 0.12 b	1.44 ± 0.16 a	22.2 ± 5.87 a	2.97 ± 1.95 a
November 1	1.27 ± 0.04 b	1.52 ± 0.05 a	1.93 ± 0.16 a	12.6 ± 1.75 a	3.57 ± 1.7 a
July 15	1.41 ± 0.02 a	0.81 ± 0.14 b	1.57 ± 0.08 a	8.6 ± 2.21 a	1.18 ± 0.55 a

Appendix 3.1.Site diagram detailing layout of 1 of 3 replicate sites used in the study. Each treatment area (Control, Nov.1, and July 15) was 0.2ha (1/2 acre) in size. Vegetation and seedling plot (O) was 1.5m x 1.5m while each seed trap(●) was 0.5m x 0.5m. Canopy openness (light) was measured at 1m above the ground at each vegetation plot (O).



Appendix 3.2. % cover of species found by treatment (November 1, July 15 & control)

Scientific name	Common name	Control (% cover)	November (% cover)	July (% cover)
Gramineae	grass	14.19	2.68	1.99
Carex pensylvanica	sedge	13.56	2.55	1.68
Rubus spp. *	raspberry	5.18	0.75	3.00
Rubus hispidus *	dewberry	4.00	0.00	0.00
Adiantum pedatum	maidenhair fern	3.00	2.50	1.00
Ribes spp.	gooseberry	2.50	1.08	0.00
Fragaria spp.	strawberry	2.44	1.31	1.25
Carex pedunculata	pedunculata sedge	2.38	1.02	1.06
Violet palmata	violet	2.22	1.78	0.77
Mentha spp.	mint	2.20	0.50	0.92
Dryopteris spinulosa	shield fern	2.00	1.33	0.00
Plantago spp.	plaintain	1.69	1.50	4.59
Hepatica acutiloba	sharp lobed hepatica	1.68	1.75	1.30
Sambucus pubens	red elder	1.60	0.00	0.00
Aralia nudicaulis	wild sarsaparilla	1.50	0.90	0.50
Cirsium spp. *	thisle	1.50	1.00	1.08
Solidago spp. *	goldenrod	1.50	6.55	1.00
Aquilegia canadensis	columbine	1.34	1.50	0.75
Mitella spp.	miterwort	1.33	1.25	0.50
Sambucus canadensis	elderberry	1.33	0.00	0.00
Uvularia grandiflora	bellwort	1.33	0.00	0.00
Taraxacum officinale *	dandelion	1.21	1.07	0.81
Laportea canadensis *	nettle	1.21	1.25	0.92
Acer saccharum	sugar maple	1.13	2.17	1.40
Lactuca canadensis	wild lettuce	1.08	1.11	0.50
Galium boreale	bedstraw	1.06	1.01	0.88
Ranuculata sp.	buttercup	1.01	1.51	1.67
Arisaema atrorubens	jack in the pulpit	1.00	1.94	1.00
Asclepias spp. *	milkweed	1.00	0.00	0.00
Oxalis montane	wood sorrel	1.00	0.88	1.00
Botrychium virginianum	rattlesnake fern	0.97	1.04	0.75
Osmorhiza claytoni	sweet cicely	0.96	1.11	0.50
Trillium grandiflorum	trillium	0.83	1.75	0.50
Hieracium spp.	hawkweed	0.75	0.88	0.50
Allium triococcum	leek	0.70	0.50	0.64

Prunus serotina	black cherry	0.67	0.67	0.75
Maianthemum canadensis	wild lily of the valley	0.58	0.84	0.75
Ostrya virginiana	ironwood	0.57	1.04	0.56
Abies balsamea	balsam fir	0.50	0.83	0.57
Acer rubrum	red maple	0.50	0.00	0.50
Aster macrophyllus	large leaf aster	0.50	0.00	0.00
Cerastium spp. *	mouse-eared chickweed	0.50	8.00	2.25
Fraxinus american	white ash	0.50	1.00	0.00
Lonicera canadensis	honeysuckle	0.50	0.00	0.50
Mitchella repens	partridge berry	0.50	0.50	2.75
Picea glauca	white spruce	0.50	0.50	0.50
Polyginatum pubescens	hairy solomon's seal	0.50	0.66	0.79
Smilacina racimosa	false solomon's seal	0.50	0.00	0.00
Thuja occidentalis	northern white cedar	0.50	0.00	0.00
Tsuga canadensis	hemlock	0.50	0.50	0.00
Anaphalis margaritacea *	pearly everlasting	0.00	0.00	0.50
Arctium minus *	burdock	0.00	0.00	0.50
Aster spp.	new england aster	0.00	0.63	0.00
Botrychium dissectum	grape fern	0.00	0.50	0.00
Caulophyllum thalictroides	blue cohosh	0.00	0.50	0.00
Cephalanthus occidentalis	button bush	0.00	2.00	0.00
Convoulvulus arvensis *	bindweed	0.00	1.00	2.00
Crucifer spp. *	mustard	0.00	3.00	1.00
Dennstaedtia punctilobula	hay scented fern	0.00	0.50	0.00
Dentaria spp.	toothwort	0.00	0.58	1.00
Equisetum spp.	horsetail	0.00	2.75	0.00
Erigeron spp. *	daisy	0.00	2.25	0.00
Erodium spp. *	stork's bill	0.00	0.50	0.00
Linaria spp.	toadflax	0.00	0.50	0.00
Myosotis spp. *	forget-me-not	0.00	0.00	3.00
Tiarella cordifolia	foamflower	0.00	1.00	2.00
Tilia americana	basswood	0.00	0.67	0.63
Ulmus americana	elm	0.00	0.56	1.00
Verbascum thapsus *	mullen	0.00	4.50	1.70
Total cover		90.21	82.13	55.70

Chapter 4

CAREX PENSYLVANICA HAS GREATER SURVIVORSHIP THAN *ACER SACCHARUM* SEEDLINGS FOLLOWING COMPETITION INDUCED SOIL WATER DEFICITS.

Executive summary

Thick *Carex pensylvanica* mats can dominate managed temperate hardwood forest understories. In these systems, *Carex* is thought to reduce the establishment and growth of tree seedlings via competition for water and/or nutrients. Here, I quantify *Carex* impacts on soil water, inorganic nitrogen and *Acer saccharum* seedling survival and growth. Potted plants grown in monocultures and *Carex-Acer* mixtures were given drought and well-watered treatments. For drought treatments, water was withheld until complete stomatal closure for each pot. I found that plant water potentials were similar at stomatal closure for *Carex* and *Acer*. However, *Carex* survival was nearly 100% in drought and well-watered treatments, whereas *Acer* survival was 90% in well-watered treatments but < 50% in drought treatments. Similarly, *Carex* mass was unaffected by drought, but *Acer* seedling mass was 25% less and height growth 40% less in drought treatments the year after the drought. Soil in *Carex* monoculture pots had 50% greater NO_3-N than soil in *Acer* monoculture, whereas NH_4^+-N concentrations were four-fold greater than NO_3-N, and did not vary among treatments. Collectively, data indicate that *Carex* growth and survival is less impacted by a given level of drought than *Acer* seedlings. Thus a well-established *Carex* understory could negatively impact tree

seedling establishment by, reducing soil moisture to levels that compromise tree seedling, survival and growth.

Introduction

In the Great Lakes region, forests with a long history of selective harvesting and high deer densities (selective browsing due to silica levels Prychid et al., 2003) are often characterized by dense *Carex pensylvanica* Lam. (Pennsylvania sedge) understories with little tree regeneration. Selective harvesting every 8-15 years does not allow for sustained canopy closure to lower light levels and reduce *Carex* populations (lower light levels measured in the understory had lower sedge cover – Randall Chapter 3). In a field experiment that included vegetation removal treatments I found that while deer browsing had the greatest negative effect on tree seedling growth and survival, *Carex* also negatively impacted tree seedling growth and survival (Randall Chapter 2). This raises the possibility that *Carex* may slow forest succession and the reestablishment of deer sensitive species, even if deer numbers are reduced (Stromayer and Warren 1997, Augustine et al., 1998, de la Cretaz and Kelty 1999, George and Bazzaz 1999).

Competition mechanisms altering tree seedling survival and growth are not well studied for systems dominated by upland sedge (*Carex*). Because of to the similarities in structure and function between grasses and upland *Carex* species, I utilized the existing grass competition literature to provide a basis for this work with *Carex*. Moreover, in studies using herbaceous plants of similar stature, competition for nutrients and moisture had greater impacts to young plant survivorship and growth than did light (Kosola and Gross 1999, Wilson and Tilman 1993). It is unlikely that *Carex* outcompetes seedlings of species with large germinants, like *Acer* and *Quercus,* for light as young tree seedlings and *Carex* grow in the same forest understory stratum (Chapter 1,2, & 3). It is more likely that in this sedge/seedling system, much like grassland dominated areas, belowground resource competition for moisture is the primary mechanism limiting tree seedling growth and survival (Davis et al., 1999 & 2005).

Competition studies (see Casper and Jackson's review -Plant Competition Underground) have been conducted in multiple systems (grassland, old-field, savanna, conifer & deciduous forests) quantifying seedling growth and survival under varying regimes of moisture, nutrient, and light availabilities. These differing regimes alter the intensity and outcomes of plant-plant competition (Sims and Mueller-Dombois 1968, Davis et al. 1999 & 2005, Wilson and Tilman 1993, Scholes and Archer 1997).

Carex, which allocates approximately 80% of its biomass below ground to roots and rhizomes (chapter 4) has the ability to share nutrients and moisture between genet and ramet, thus increasing young plant survivorship in times of stress (de Kroon et al., 1998). In contrast, tree seedlings are not connected to their parents. Furthermore as tree seedlings grow they rapidly extend roots into deeper zones than grasses and *Carex* to obtain moisture and nutrients. However, young seedlings, and seedlings stressed by factors such as browsing (Frank and Evans 1997) and low light (J.M. Kunkle, M.B. Walters, R.K. Kobe, unpublished data) can have most of their roots in shallow surface zones, potentially increasing their competitive interactions with *Carex* and other herbs (Knoop and Walker 1985, Dodd et al., 1998). Increased survivorship, growth (Elliott and White 1987, Davis et al. 1999, Gordon and Rice 2000), and recruitment (*Pseudotsuga menziesii*- Dunne and Parker 1999), have often been observed for tree seedlings when competing vegetation was removed or when water was added (Harrington 1991, Davis et al. 1999). Conversely, some studies have reported that soil water potential did not change when surrounding vegetation cover was removed (Coates et al., 1991), and that soil moisture did not negatively impact seedling density (Maguire and Forman 1983). Berkowitz et al., (1995) even suggests that surrounding vegetation might buffer young seedlings during periods of drought.

Several factors could contribute to the lack of generality in the results of these studies: variation in vegetation density and physiology, climate (precipitation, evaporative demand), and soils. Nonetheless, it is clear that competition for water can limit tree seedling growth and survival in some systems. It is less clear how this competition occurs. Superior competitors: 1) could maintain photosynthesis and transpiration (and thus growth) at lower water potentials, potentially conferring a growth advantage; 2), by maintaining photosynthesis/transpiration at lower plant water potentials, could diminish soil water potentials to levels jeopardizing the survival of less drought tolerant species (Tilman 1982); 3) could better tolerate (i.e. survive) the effects of a given level of stress (drought) (Grime 1977).

In addition to water, sedge could out-compete tree seedlings for nutrients, including nitrogen (N), the most frequently limiting nutrient in temperate terrestrial systems, but to date, data are sparse. Possible mechanisms for *Carex* effects on N include 1) *Carex* being able to reduce mineral soil N to levels inadequate for tree seedling growth and survival (Wedin and Tilman 1993), and/or 2) *Carex* altering available N (e.g. NO_3^-, NH_4^+, organic N) to forms that tree seedlings can not use as effectively or by sequestering substantial N resources in rhizomes and utilizing those stored resources to rapidly replace tissue lost due to browsing (Bryant et al., 1983)

Can competition for water help explain Carex's negative impacts on tree seedling growth and survival found in the field? Specifically, 1) Can *Carex* draw soil water to lower levels than *Acer saccharum* seedlings? 2) Does *Carex* have greater survivorship than *A. saccharum* seedlings at low water availability? 3) Does a drought event negatively affect *A. saccharum* growth? In addition, I asked, does *Carex* negatively affect soil mineral nitrogen availability? I examined these questions with a three-year potted plant experiment that included monocultures and combinations of *Acer saccharum* seedlings and *Carex pensylvanica* culms, either well-watered or subject to a single dry-down treatment during the second growing season. Water was withheld until stomatal closure for either *Carex* or *Acer* in both combination pots and monoculture pots. Survival and growth for seedlings were monitored through the third growing season.

Methods.

Design and Materials

In November of 2000, *Acer* seed was collected from Western New York which was in the same USDA hardiness zone (4b) that sedge was collected from, mixed with moist perlite, and cold stratified (2-4°C) in ziplock® bags. As I was interested in the effects of drought, I chose to use a soil that would not hold excess soil water for extended periods of time. In late March 2001, a relatively infertile field soil was collected from just below the A horizon on a sandy outwash plain in southern Roscommon County, MI. Soils in the region are a mixture of Rubicon – Menominee, and Graycalm and Grayling sands (USDA soil survey of Gladwin County 1972 and Roscommon County 1972). Sites typically support stands of aspen (mixed *Populus tremuloides* and *P. grandedentada*) and Oaks (*Quercus alba*, *Q. vellutina*).

In early April 2001, *Acer* seeds with emerging radicles were planted into nursery trays (12.7 cm depth X 6.4 cm diameter) filled with field soil, and allowed to establish for three weeks in the MSU Tree Research Center greenhouse under 18 hr /6 hr (day length / night length) conditions. *Carex* culm mats were collected in early April from the same location that field soil was collected, transported to the Tree Research Center where they were slowly warmed to 21°C allowing them to break winter dormancy, and were maintained at field water holding capacity for three weeks under the same greenhouse environment as germinating *Acer* seeds.

Individual *Carex* culms (consisting of a single rhizome and root not exceeding 5 cm in length) and three week old seedlings were planted as monocultures (n=4 plants) or combinations (1 *Acer* and 3 *Carex* culms) in Poly-tainer ® 2-gallon pots filled with homogenized infertile field soil. Pots were allowed to establish in the greenhouse until June 15th 2001, at which time they were fertilized with a three-month slow release fertilizer (Osmocote 15,15,15 at the rate of 200kg N/ha), and transferred to an outdoor lathe house (50% shade) for a one-year establishment period. I randomly assigned replicate pots from each vegetation treatment (see Table 4.1 for explanation) to a drought treatment (well-watered/water withheld) and to two harvests (First harvest = the morning after the designated stomatal closure point was reached, and Final harvest = after leaf drop following the subsequent growing season). The 160 pots were grown under 50% shade lathe with well-watered conditions until August 12th 2002, at which time I began drought treatments by excluding both rain and supplemental watering on the appropriate drought pots. At this time I harvested 2 or 3 pots each of *Acer*, *Carex*, and *Acer-Carex* pots and found roots to be abundant and well distributed throughout the soil volume in all treatments, suggesting that drought treatments should result in more or less homogeneous soil water deficits within the soil volume. In addition, for the duration of the experiment

Acer leaf canopies were at or above the height of *Carex* in mixed pots indicating that competition for light was likely minimal.

Due to concerns over a potentially serious experimental design flaw which were raised during the review of this section I provide justification for the validity of the results using a secondary study. The concern originated because I used seed from a western New York source (hardiness zone 4b-5a) and planted the developing young sugar maple seedlings into sedge and soil collected from an ice contact/sandy outwash region in the northern lower peninsula of Michigan (USDA hardiness zone 5a). Sugar maple forests are not commonly associated with these ice contact/outwash sites and as such it is possible that the sedge plants that I collected and used had adapted to their original soils, thus conferring an advantage to sedge. Concerned with this possibility, I reran the entire study the following year using soil, sugar maple seed, and intact sedge culms all collected from a site in the Upper Peninsula of Michigan. In the follow-up study, sedge was found to close their stomates at more negative internal plant water contents than sedge from the ice contact /sandy outwash plain (-6.8 MPa vs. -5.1 MPa), respectively. If the sedge plants used in the original study were adapted to the xeric soil conditions associated with outwash and ice contact landforms, and were therefore functionally different than sedge found growing in the understory of productive mesic sugar maple stands, I believe that sedge stomatal closure points would have reflected these differences. Specifically, Sedge closure should have occurred at more negative not less negative internal moisture potentials when compared to sedge from mesic hardwood sites, and they did not. I therefore feel confident that the results I obtained do highlight unbiased differences in sedge and sugar maple responses to drought and competition.

Plant measurements pre/post harvest

During the dry-down period leaf transpiration was measured daily for all water withheld treatment pots and every other day for well-watered pots with several Li-Cor 1600 steady state porometers (Li-Cor Inc., Lincoln NE). Drought treatments continued on an individual pot basis until stomates closed for the target (i.e. assigned treatment) species (Table 4.1). For each of the drought and well-watered control pots assigned to be destructively harvested in the first round, I estimated plant water status for each individual with predawn Scholander pressure bomb measurements of xylem water potential the morning after stomatal closure. Drought pots not selected for the first harvest were rehydrated when they reached stomatal closure. Following the drought treatment, all remaining well-watered and drought pots were maintained under well-watered conditions, overwintered in a hoophouse, and measured for spring and fall seedling survival and growth during the following growing season. For both *Acer* and *Carex*, survival was measured on an individual seedling or *Carex* culm basis. Final harvests were conducted in late fall 2003 after *Acer* leaf drop.

At all harvests, I determined for each plant organ and species respectively, above and below ground plant mass, N concentration, N content, as well as leaf area and total root length). For *Acer*, I also measured annual height & diameter growth increment. Nitrogen concentration was measured by the Dumas combustion method on a CN analyzer (Carol-Erba, Milan, Italy).

Soil Resource Measurements

Immediately following the first harvest, soil was collected from each harvested pot to determine KCl extractable soil nitrogen concentration. Soil from each pot was thoroughly homogenized and sieved with a 4 mm screen, subsamples were stored in ziplock® bags at 1°C, extracted within 5 days with 2M KCl (20 g field moist soil with 50 ml KCl) on a shaker table for one hour, and allowed to settle for 30 minutes before being filtered through Whatman® #42 filter paper. At the time of each extraction, soil moisture was determined gravimetrically so that I could relate these measures directly to plant water status measurements and to allow calculation of NO_3^--N and NH_4^+-N on a per unit dry soil basis. All extracts were refrigerated until being measured for NO_3^--N and NH_4^+-N (within 30 days of extraction) on an OI Alpkem Autoanalyzer (OI Analytical, College Station, TX) by phenol-hypochlorite and cadmium reduction methods, respectively.

Analysis

Initially, 160 pots where divided into four groups of 40 pots and were randomly assigned to one of four species treatments (*Acer* monocultures, *Carex* monocultures, *Acer-Carex* combination pots dried to the stomatal closure point of *Carex*, and *Acer-Carex* combination pots dried to the stomatal closure point of *Acer*). Within each of the four species treatments (~40 pots/species treatment), pots were randomly assigned to either a water or no water treatment. Prior to withholding water resources, pots were visually evaluated for uniformity in *Acer* seedling and *Carex* culm numbers per monoculture pot and pots that were non-uniform were discarded from the study. Of the remaining 154 pots, six pots in each species treatment by water/no water drought treatment were randomly assigned to the first harvest (total N = 48) and all remaining pots in each species treatment by water/no water drought treatment (N = ~14 pots) were designated as final harvest pots.

For analysis, species and drought treatments were considered discrete, nominal variables. Main effects and interactions of species treatment and water/no water for plant stomatal conductance, above-ground (total seedling and *Carex* mass, organ mass, leaf area, and stem length for *Acer*) and below-ground growth characteristics (mass, total root length) and soil (Extractable N, water content) were analyzed with least squares models using JMP 5.1 statistical software (SAS Institute, Cary, NC, USA). Using water / no water and species treatments as covariate predictors, I modeled seedling survival with Cox's proportional hazards methods (Cox 1972). Tukey's HSD was used to test for significant differences among water/no water and species treatments for plant and soil characteristics. When interaction terms were insignificant beyond the threshold suggested for pooling variances ($P > 0.25$, Bancroft 1964), the highest order interaction term with the highest P value was removed and the model was re-run. This process was repeated iteratively until a final model was constructed where all interactions >0.25 were removed.

Results

Stomatal conductance

Seasonal variation in *Acer* and *Carex* photosynthetic capacity was clearly evident as conductance declined for both *Carex* and *Acer* in the well-watered controls over the course of the study (Julian date 226-261, Figure 4.1A & B, Table 4.2). For water withheld treatments, *Acer, Carex* and *Acer-Carex* mixtures reached their respective significant conductance differentiation point from well-watered control treatments between Julian dates 245 – 248 for *Acer* and Julian dates 247 – 250 for *Carex* following the commencement of withholding water. All pots exposed to the induced drought event reached their respective stomatal closure points within a three-day period (Julian days 258 - 260).

Vegetation and soil resource measurements corresponding to drought severity

At stomatal closure, droughted *Carex* and *Acer* monocultures had similar predawn water potentials (approximately –5MPa, P=0.8091). Mean *Acer* monoculture predawn moisture potential (MPa) was significantly lower than *Acer* seedlings in combination pots at stomatal closure (Figure 4.2A, Table 4.3B), while *Carex* showed mixed results. Specifically, pots that were harvested when *Carex* closed their stomates had similar moisture potentials to *Carex* monocultures, while pots harvested when *Acer* stomates closed had significantly less negative potentials than *Carex* monocultures. (Figure 4.2B, Table 4.3C) Gravimetric soil water was similar among all well-watered treatments and likewise for all drought treatments (Figure 4.2C., Table 4.3A.). Well-watered *Acer* monocultures had significantly lower soil nitrate concentrations than well-watered *Carex* monocultures and combination pots (Figure 4.2D., Table 4.3D.). However ammonium concentrations were 6.2 fold greater than nitrate across all treatments and were unaffected by water or species treatments (Figure 4.2E, Table 4.3E.).

Survival

Acer seedlings grown in monoculture or mixed with Carex had similar and high survivorship (Figure 4.3A.). While there was a trend for droughted seedlings grown in combination with *Carex* to have lower survival (30%) than those from seedling monocultures (50%), differences were not significant. Interestingly, *Carex* survival was unaffected by drought, surviving equally under well-watered and drought conditions (Figure 4.3B).

Size, morphology, and N concentrations

Drought did not affect *Acer* (p=0.3950) or *Carex* (p=0.5403) total root length one year after the induced drought. In contrast, one year after the drought *Acer* mass was 23.6 % lower (Figure 4.4, P=0.0025), the subsequent growing season stem extension growth was 52% lower (P=0.0006), and drought had no effect on *Carex* mass (Figure 4.4, P=0.1213). Furthermore, drought did not affect root mass ratio, leaf mass ratio, specific root length, leaf area ratio, and specific leaf area, for either *Acer* or *Carex* except that specific leaf area (m^2/g) declined in response to drought for *Carex* (SS=187.5, F Ratio= 10.9, P=0.0025). Although we measured N content in plant organs immediately following the drought, no clear pattern was discernable. I did, however, find that seedlings grown in species combinations had higher concentrations of N in leaves, stems, and roots compared to monocultures, while *Carex* had lower foliar and root N concentrations in combination pots.

Discussion

Acer and *Carex* had virtually identical predawn plant water levels when grown as monocultures, but *Acer* survival was roughly 50 % lower than monocultures of droughted *Carex* (~100% survival). For monocultures of *Acer*, seedlings closed their stomates at predawn moisture contents that were near their lethal leaf water potential (-5.76 MPa - Auge et al., 1998). Although not significantly different than droughted monocultures, *Acer* survival was more variable and trended lower in droughted combination pots, especially when rehydration occurred at *Acer* stomatal closure. Seedlings in combination pots seem to "sense" the presence of *Carex* and regardless of the point of rehydration (*Carex* (A c-) or *Acer* (a C-) stomatal closure), close their stomates at significantly less negative predawn moisture contents (approximately 40% less negative than droughted *Acer* monocultures). Adding to the inconclusiveness of the results, seedling survival trended lower in pots where rehydration occurred at seedling not *Carex* stomatal closure. The shift in lower survival in combination pots with less negative water potentials does not correlate with the lethal leaf water potentials put forth earlier. Taken at face value, one would be inclined to surmise that seedling survival would have increased in these combination pots if moisture content was the driving mechanism. As I did not see stomatal conductance measurements decline more rapidly or complete stomatal closure occur earlier in the combination pots, I concluded that seedlings were exposed to equivalent drought acclimation periods.

Immediately following the first harvest, soil samples revealed that extractable NO_3^- -N levels were significantly lower in well-watered *Acer* than well-watered *Carex* monocultures or combination pots. This contradicts Templer and Dawson's (2004) work, which showed *Acer* as preferential using soil NH_4^+ -N more than NO_3^- -N. This result needs to be viewed carefully as the overall levels of soil NH_4^+ -N were six times as great as NO_3^- -N and showed no effect of water/no water treatments or species treatments. However, variable NO_3^- -N levels in the pot microcosms are in contrast to results from a field study which looked at areas with higher vs. lower deer densities and found that at higher deer densities, which also had three times the *Carex* biomass, had soil NO_3^- -N levels that were constant, whereas NH_4^+ -N levels almost doubled (Chapter 1). One concern in comparing the two studies is that field sites were aspen dominated monocultures with very little, if any, *Acer* trees attaining intermediate canopy levels in these stands and thus overstory demands for differing forms of N may have driven the differences. If, as this greenhouse study shows, *Carex* does not utilize available NO_3^- -N to levels that are lower than those of *Acer* monocultures and has no effect on NH_4^+ -N, one might conclude that overabundant *Carex* does not reduce nutrients to levels that are lethal to *Acer*.

While most of the organ level N results were mixed and unclear, foliar N concentrations increased in *Acer* combination pots by 20% vs. *Acer* monocultures, while *Carex* N concentrations decline 11% in combination vs. monocultures pots. The differing reaction to the presence or absence of competitors by *Acer* and *Carex* suggests that in areas with high *Carex* densities and regenerating *Acer*, seedlings become more palatable to deer while *Carex*, which is already quite unpalatable (high silica contents- Prychid et al. 2003), becomes even less palatable. The negative drought effects on sedge leaf and root mass in combination pots were short lived, failing to be significant one year after the induced drought. For surviving *Acer* seedlings, drought had no effect on growth the year of the drought, but growth of seedlings was reduced the year after drought by 27%.

Tilman's R* model was not supported by the *Carex* X *Acer* interactions in this study. *Carex* (the surviving plant) did not reduce soil moisture or nutrient resources to lower levels in combination pots. In fact, *Acer* monocultures reduced $NO3^-$ - N levels below *Carex* monocultures and combination treatments. Even thought *Carex* internal water potentials were lower than *Acer* water potentials in both combination treatments at stomatal closure, both *Carex* and *Acer* in combination had, for the most part, less negative potentials than their respective droughted monocultures. Again, seeming to not support Tilman's R* theory.

In this study, *Carex* seems to be both a good competitor and a good stress tolerator. *Carex*'s ability to 1. rapidly usurp belowground space (1000+ m of roots by year three for *Carex* vs. 18m for *Acer*), 2. protect itself from browsing through structural means (intercalary meristem) & high foliar silica contents- Prychid et al.,2003) and differential partitioning of resources to protected areas (80%+ of biomass is belowground) and 3. Possibly consume luxury amounts of nutrients while storing the nutrients in rhizomes giving it more of an advantage in periods of resource limitation, makes sedge a great competitor. But, the uniformity in which *Acer* and *Carex* respond to soil resource availabilities (equivalent internal moisture points in monocultures at stomatal closure), and the differing survival responses to drought also means that *Carex* could be labeled as a stress tolerant (Grime 1977).

In short, *Carex*, either as monocultures or in combination with *Acer* seedlings can competed for nutrients and moisture resources and survive drought events much better than *Acer*. Even thought *Acer* closed their stomates at a less negative water potentials in the presences of sedge, survival was still compromised. Over time, as *Acer* seedlings fail to survive and are replaced in the system with the established, surviving, clonal growth of *Carex*, it may become more difficult for seedlings to acquire the needed resources (moisture, nutrients, light, space) to survive (initial advantage altering competition – Wilson 1988, Gurevitch et al., 1990). We can only postulate, but subsequent drought events may have even greater impacts on seedling survival.

Summary

Continued use of a short rotation (8-15 years) selection based harvesting in northern hardwood forests with elevated deer populations virtually assures that high coverage of *Carex* will remain, if not expand. This study shows that sedge has the potential to greatly reduce the number of seedlings in the forest understory following a single drought event. Given the lack of information concerning impacts to seedling survival following subsequent drought events in these systems, and the potential that drought has cumulative impacts on seedlings survival, it is possible that virtual all sugar maple seedlings could be eliminated from the understory prior to attaining a tall enough stature to be considered browse for deer. For systems at least in Michigan, it is not uncommon for mid-summer drought events to occur yearly or every other year (NOAA NCDC weather data). Furthermore, for those seedlings that do survive single or multiple drought events, *Carex* induced water deficits may decrease and, in some extreme cases, halt the extension growth of young seedlings completely (chapter 2 & 4). Cessation of growth could place seedlings in an almost perpetual state of herbivory, adding yet more stress to young seedlings.

Contrary to work by Pastor et al., (1993 & 1998) I did not find large shifts in belowground resources with the addition of a "lower" quality species. The fact that *Carex* and *Acer* have 1) similar stomatal responses to drought at roughly equivalent internal moisture levels in monocultures, 2) similar levels of soil water in monocultures and combination pots at stomatal closure, and 3) the surviving species (*Carex*) does not reduce soil nutrient resources to lower levels than *Acer* seems to more closely fit Grime's CSR theory than Tilman's R* model. More work is needed detailing the interactive effects of competing species (*Carex* vs. *Acer*) under varying light regimes as light has previously been shown to alter oak and grass competitive responses to drought (Davis et al. 1999) and, more specifically, under low light conditions *Acer* may better tolerate drought than *Carex*, while under high light, the reverse may be true.

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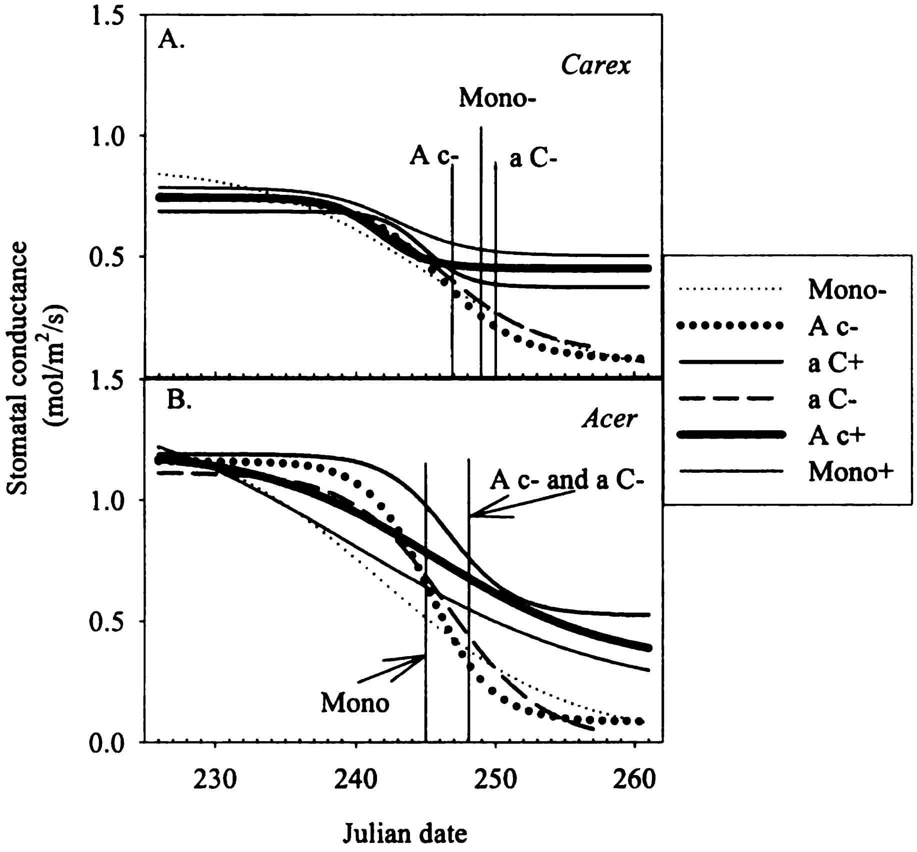

Figure 4.1. Daily *Acer* and *Carex* stomatal conductance (mol/m^2/s) by treatment over the course of the study (Julian days 226-261). Lines represent point at which water vs. water withheld treatments became significantly different (P=0.05).

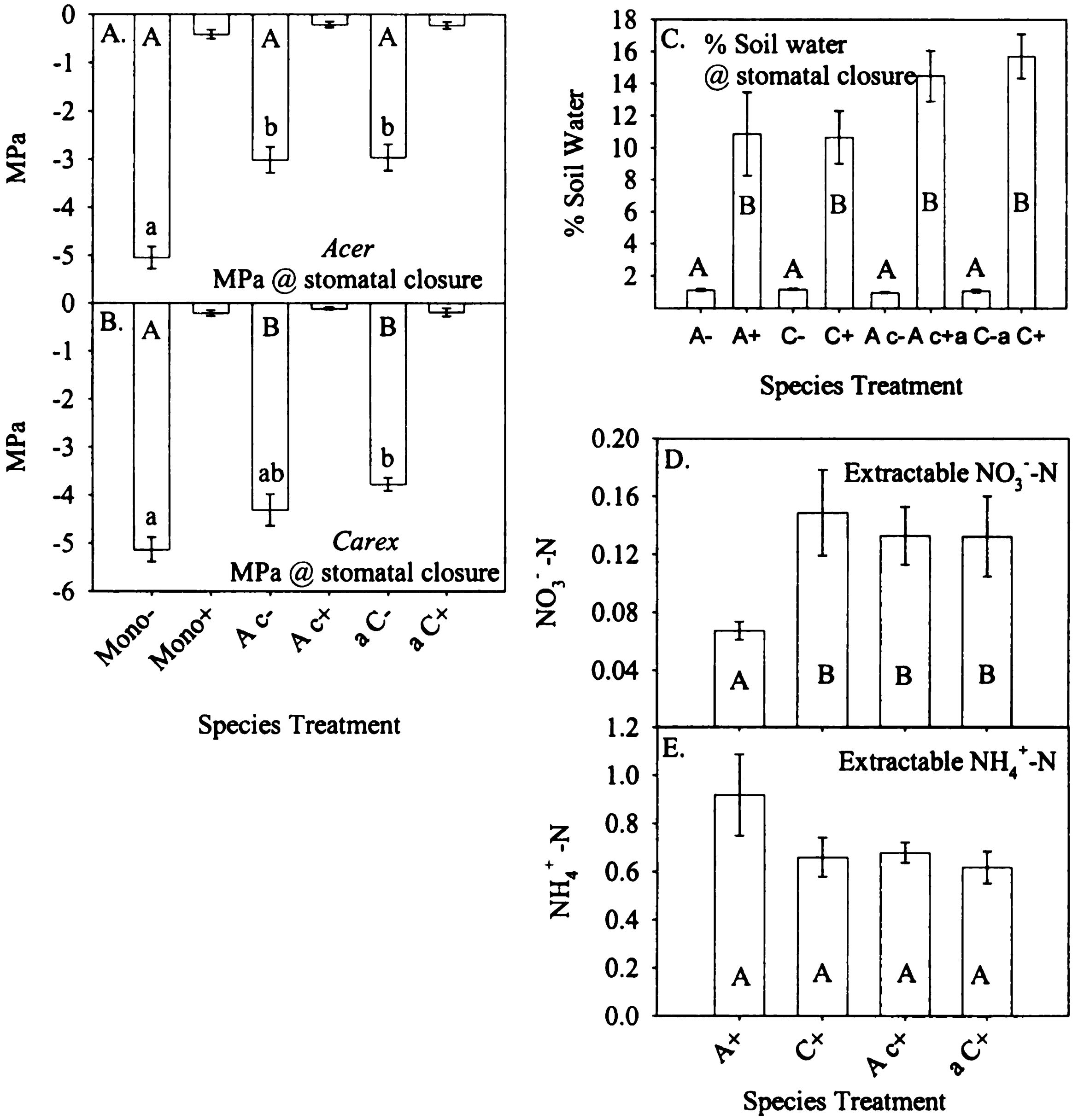

Figure 4.2. *Acer* (2A) and *Carex* (2B) predawn moisture potentials (MPa) from seedling and *Carex* culms reaching their respective stomatal closure points or from well-watered control individuals. Gravimetric soil water by treatment at the first harvest (2C). Extractable NO_3^- (2D) and NH_4^+ (2E) immediately following the first harvest. Error bars represent ±1 St. Error. Large cap letters in 2A&B represent differences between *Acer* and *Carex* within a given species treatment, while small cap letters represent differences (P=0.05) in species treatments within either *Acer* or *Carex*. In 2C, large cap letters represent differences (P=0.05) between water and no water treatments. Large cap letters represent differences in either extractable $N0_3^-$ -N (2D) or NH_4^+ - N (2E) across well-watered treatments.

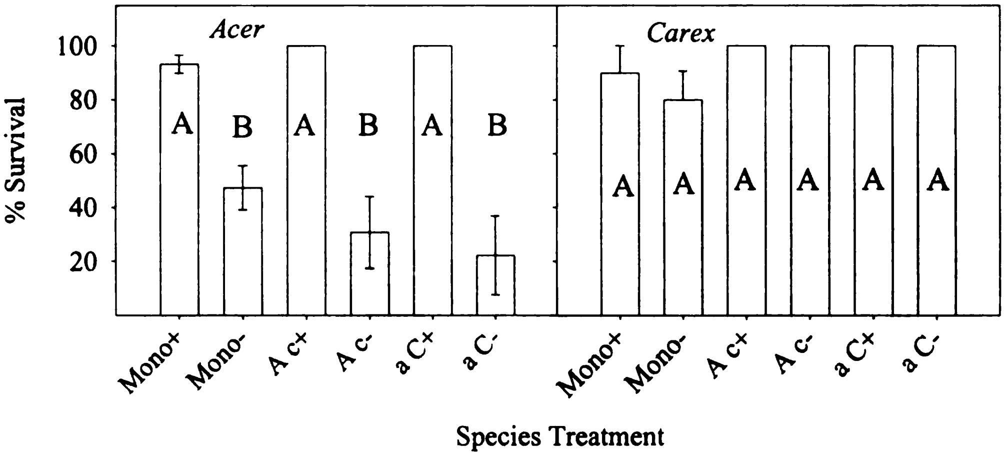

Figure 4.3. *Acer* (3A) and *Carex* (3B) survival one year after an induced drought event. Error bars represent ±1 St. Error. Letters represent differences (P=0.05) in survival across species treatments within *Acer* or *Carex*.

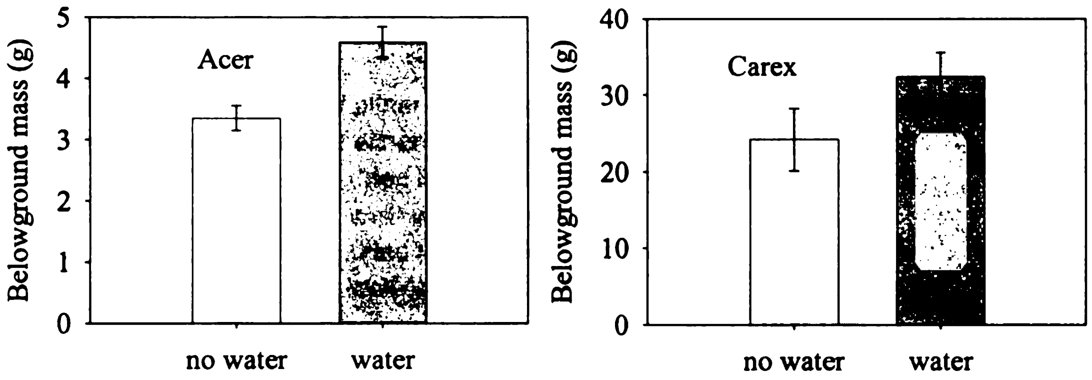

Figure 4.4. *Acer* and Carex belowground growth by water / water withheld treatments.

Table 4.1. Explanation of treatments used in the study.

Treatment ID	
Mono-	Monocultures of either *Carex* or *Acer*, dried to their respective stomatal closure points
Mono+	Monocultures of either *Carex* or *Acer*, well- watered controls
A c-	1 *Acer* 3 *Carex*, dried to the stomatal closure point of *Carex*
A c+	1 *Acer* 3 *Carex*, well- watered controls for A c-
a C-	1 *Acer* 3 *Carex*, dried to the stomatal closure point of *Acer*
a C+	1 *Acer* 3 *Carex*, well- watered controls for a C-

Table 4.2. Results of a standard least squares mixed model for the effects of water/no water, species treatment, date, and their interactions on *Acer* and *Carex* stomatal conductance. Interactions with P>0.25 were pooled with the error term (Bancroft 1964) and the models rerun.

Stomatal conductance	Anova effects	SS	F	P
Acer	Water/No Water	0.3353	31.5112	**<0.0001**
	Species Treatment	0.2377	11.171	**<0.0001**
	WxST	0.0733	3.4469	**0.0321**
	Date	8.0169	753.529	**<0.0001**
	WxD	0.5572	52.3706	**<0.0001**
	STxD	0.0384	1.8062	**0.1647**
	WxSTxD	0.1171	5.5025	**0.0042**
	Adj. R^2			0.4344
Carex	Water/No Water	0.2311	46.6571	**<0.0001**
	Species Treatment	0.0346	3.4891	**0.0307**
	WxST	0.0472	4.7633	**0.0086**
	Date	2.7134	547.926	**<0.0001**
	WxD	0.3255	65.7348	**<0.0001**
	STxD	0.0018	0.186	0.8303
	WxSTxD	0.0078	0.7919	0.4531
	Adj. R^2			0.3371

Table 4.3. Results of a standard least squares mixed model for the effects of water/no water, species treatment, and their interaction on gravimetric soil moisture (3A), predawn seedling moisture potential (3B), predawn *Carex* moisture potential (3C), and standing pools of $N0_3^-$ (3D) and NH_4^+ (3E) at the point of stomatal closure.

1.Stomatal closur	Source	DF	SS	F Ratio	P>F
A. Soil Water	Water/No Water	1	1592.5	173.48	**<0.0001**
	Species Treatment	3	56.055	2.0354	0.1252
	WxST	3	61.523	2.234	0.1
	Adj R^2				0.7618
B. *Acer* water Potential	Water/No Water	1	9877.6	439.34	**<0.0001**
	Species Treatment	2	955.13	21.24	**<0.0001**
	WxST	2	718.16	5.97	**<0.0001**
	Adj R^2				0.9376
C. *Carex* water Potential	Water/No Water	1	16120.5	800.47	**<0.0001**
	Species Treatment	2	295.63	7.34	**0.0025**
	WxST	2	269.41	6.69	**0.004**
	Adj R^2				0.9592
D. NO_3- -N	Water/No Water	1	0.2817	1.921	0.1738
	Species Treatment	3	3.5773	8.085	**0.0003**
	WxST	3	1.4281	3.2456	**0.0324**
	Adj R^2				0.3902
E. NH_4+ -N	Water/No Water	1	0.0014	0.052	0.8209
	Species Treatment	3	0.068	0.8332	0.484
	WxST	3	0.1517	1.8601	0.1528
	Adj R^2				0.0143

Table 4.4. ANOVA results for plant water potential testing between *Acer* and *Carex* within a given species treatment (monoculture, A c, a C). only for no water treatment individuals.

	Source	DF	SS	F Ratio	P>F
Monocultures	Species	1	0.021888	0.0617	0.8089
	Error	10	3.54971		
	C. Total	11	3.5716		
A c	Species	1	5.005208	9.1832	0.0127
	Error	10	5.450417		
	C. Total	11	10.455625		
a C	Species	1	1.960208	7.1226	0.0235
	Error	10	2.75208		
	C. Total	11	4.71229		

Conclusions by chapter

I. *Impacts to aspen understory structure and composition across site productivity and stand age gradients in higher and lower deer density areas.*

Deer have altered the understory composition of forbs and seedlings, and have directly reduced the structural characteristics of future stands. Although stand age and site productivity did explain some responses, their lack of interaction effects with deer focused most of the discussion and management implications on elevated deer density effects. Specifically this study found that:

- Levels of non-browsed (unpalatable) species (sedge and fern) have tripled on sites with higher relative deer densities across the entire range of site productivities, increasing aboveground (light) and belowground (soil water, nutrients, and space) resource competition between these species and establishing seedlings.
- While higher relative deer densities have reduced forb biomass in aspen stands to 1/10th that of lower, more moderate deer density areas, seedling stem densities (0-0.6m tall) have remained constant.
- Compositionally, deer have simplified forb and seedling layers having greater negative impacts to richness on more productive sites. Increased red maple stem densities 0-0.6m tall, at the expense of oak and intermediate canopy species such as witch hazel, indicate a shift in the future stand composition.
- Stand management goals, objectives and methods, along with deer populations and inherent site factors, will play a part in determining stand stocking levels. As such, it would be misguiding for managers to take the results of this work and definitively state that future stands will most likely be only marginally stocked

(250-300 stems/ha) with black cherry (the only species represented in the 0.6-4m tall measurement zones).

Aspen management implications

It would be advisable for resource managers to coordinate harvesting and wildlife population management activities at a landscape level. This would allow forest managers to concentrate traditional forest harvesting activities in areas with lower deer densities and perhaps use more experimental harvesting or site treatment methods in areas with higher deer populations in hopes of minimizing or ameliorating the negative effects of deer. Resource managers need to realize that forest harvesting will, by its practice, promote an increased quantity and better quality of available deer browse, and that deer populations will respond accordingly. The potential for future deer impacts to the herbaceous layer compositions should be evaluated with site productivity in mind, and be incorporated into management plans in all stands, with preference and resources going to stands in areas with high deer densities. Furthermore, the costs, both social and on the ground, associated with stand and understory remediation will rise if steps are not taken to control the deer herd in areas of active forest management.

II. Deer and sedge impacts to vegetation dynamics in northern hardwood systems of the Upper Peninsula.

While sedge does play a minor role in altering seedling growth in areas protected from deer, enough seedlings were able to establish, survive, and grow in dense sedge areas that the I cannot target sedge as the primary cause of the regeneration failure common in these high sedge - high deer environments. Deer effects, on the other hand, dominated the system, altering understory forb and seedling compositions and outright eliminating seedling growth into height class above the zone of deer browsing. Specifically, results indicated that

- Mid summer (July) herbicide treatments are effective at reducing sedge mass (94-97% after 2 years and 50% after 4 years), providing a window of reduced vegetation competition to help tree seedlings establish. Unfortunately, tree seedlings were also susceptible to foliar herbicide application, but through seedling recruitment, biomass was not significantly different 4 years after treatment.
- While vegetation treatments did not affect forb mass, the presence or absence of deer greatly influenced herbaceous layer compositions after 4 years. Populations of *Carex*, dandelion, goldenrod, raspberry as well as seedling covers of red maple, balsam fir, and to a lesser extent, white ash increased in areas open to deer, while trillium, lily-of-the-valley, toothwort, sweet cicely, and sugar maple all increased in areas protected from deer.
- Although seedling biomass levels rebounded by year 4 in spray areas, the practice of mid summer spraying should be minimized. Summer spraying lengthens the time that it takes to get a new cohort of trees beyond the reach of deer, primarily because the new cohort must establish from seed as spraying kills advanced regeneration.
- The exclusion of deer greatly improved tree seedling survival and overall growth while herbicide treatments increase growth, especially as overstory conditions improved (increased canopy openness), but had no impact on seedling survival.

- Measured soil properties (extractable NO3- - N & NH4+ - N and N mineralization rates) were not altered by deer or vegetation manipulation treatments in this study. One might expect theses systems to be more resistant to belowground nutrient changes as the vast majority of litter influx comes via the overstory, where ungulate induced pressures are last to be felt in these systems.

Northern hardwood management implications

In selection harvested productive northern hardwood systems with elevated deer densities, the sustainability of the current forest is in question. Deer have eliminated all sugar maple regeneration in these areas and are even reducing ironwood. If forest and wildlife management practices (selection harvesting, allowing deer herds to remain elevated in areas where impacts to regeneration are already quantifiable) are not altered, systems with high deer will continue to have chronic seedling recruitment failure, and increasing loss of intermediate canopy trees and associated intermediate canopy wildlife species. Eventually, the system may lose its overstory structure, compositional diversity, and light reducing ability. The ability to reduce light through closed canopy conditions is critical in these systems if sedge is to be reduced in a manner that does not rely on chemicals. Along these same lines, forest managers should consider increasing the reentry period from the standard 8-12 years, (which is the current practice on industrial lands) to 30-35 years or more, as the longer timeframe between cuts should allow for sustained low light conditions to promote low sedge mass levels in the understory. Preferably, this would occur in tandem with a reduction in the deer herd to levels that allow for tree regeneration (~7 deer/km^2).

III. Selectively removing sedge at larger scales with timed herbicide applications

Strategically timing herbicide applications can effectively reduce populations of competing vegetation while minimizing the herbicide damage to desired tree seedlings and forbs. At a 0.2ha scale, greater deer damage was found in treated areas. Perhaps if treated areas were larger and deer feeding was not as concentrated, the positive effects of the spraying would translate into greater numbers of seedlings growing into taller height classes. Timed herbicide treatments resulted in:

- Sedge being as effectively controlled with a fall (November 1) application of herbicide when compared to a July 15 spraying, and had the added benefits of not reducing forb or seedling mass or spring ephemeral plant richness. Fall spraying increasing tree seedling germination, establishment and survival over both july15 spraying and controls.
- While levels of deer damage were higher than controls with November spraying, July spray treatments received more than twice the deer damage at higher light levels than comparable November spray areas.

Management implications to fall spraying in northern hardwood forests.

More work is needed to transfer the 0.2 ha results to a stand or landscape level. Forest managers should be cautiously optimistic about fall spraying's effectiveness at controlling sedge, but questions remain as to the viability of this treatment at larger scales when faced with elevated deer densities. Management of the landscape structure surrounding northern hardwood stands (reduction in cedar swamps) in conjunction with stand level fall applications of herbicides may be more effective than either treatment individually. Managers need to retain larger diameter seed trees and attempt to plan treatments (harvesting, spraying etc.) around good seed years. This is not always possible but, to date, fall treatments give a 2 year (possibly up to a 4 year) window of reduced plant competition before sedge reinvades and dominates the understory. Again, more work is needed at greater spatial extents, controling for surrounding landscape features (cedar swamps) but overall this work highlights the ability to use an inexpensive herbicide in the fall to control seedling competitors while not harming the seedlings themselves.

IV. Mechanisms driving the sedge – maple interaction

Although sugar maple and sedge monocultures respond similarly during drought events by closing their stomates at equivalent moisture contents, few other similarities exist between seedlings and sedge. In combination pots, sedge did not reduce soil moisture or nutrients to levels that were lethal to seedlings and maintained its dominance through its ability to survive drought events while not altering belowground growth. The potential ramifications of the observed shift in foliar N concentrations where sugar maple increased and sedge declined when sedge and maple were grown together could be a factor in why seedlings are browsed more so than sedge. This controlled environment study specifically showed that:

- Sedge and maple monocultures respond similarly to drought by closing their stomates at extremely low yet equivalent internal moisture contents. For maple, internal moisture contents at stomatal closure was close to known levels of lethal leaf water content.

- Even with the readjustment of stomatal closure shown by maple (stomates closed at less negative water potentials in combination vs. monoculture pots) and the greater reduction in extractable N by maple, sedge post drought survival was virtually 100% vs. maple seedlings, which survived 20-50% of the time.
- Droughted maples had less belowground biomass a year after the drought while sedge was unchanged, possibly indicating that in subsequent drought years seedling mortality might increase.
- Foliar N concentrations increased for sugar maple in combination pots while N concentrations decline. Although interesting, the fact that my previous work found greater browsing in areas where sedge was eliminated means that deer may be focussing on seedlings that are visually easier to find vs. ones that have higher N content. If the reverse was true, seedlings in the sedge controls should have had the highest foliar N concentrations and the greatest amount of browsing damage, which was not the case.

Management implications from sedge – maple interactions

Seedlings in the field are often exposed to multiple drought events during the understory establishment phase. It is possible that after several years and several drought events there may be very few, if any, seedlings reaching a stature that deer would then utilize. Another possible explanation is that drought induced mortality lowers the seedling population to such a low level that deer are then physically able to browse all stems. In reality, the lack of regeneration in the highly managed forests in the Upper Midwest may not be due to deer browsing alone, but rather through the combined effects of direct deer browsing on the remaining seedlings whose populations have been reduced through drought events and competition with sedge. There might also be a feedback mechanisms in place where deer induced high sedge densities promote increased levels of browsing on preferred seedlings (maple has elevated foliar N concentrations when grown with sedge) and the increased seedling browsing decreases future levels of competition (for light) that sedge will face if seedlings establish.