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THE INFLUENCE OF CONCURRENT DISTURBANCES ON PLANT COMMUNITY
DYNAMICS IN NORTHERN HEMLOCK-HARDWOOD FORESTS

By

STACIE A. HOLMES

A DISSERTATION

Submitted in partial fulfillment of the requirements

for the degree of

DOCTOR OF PHILOSOPHY

Forest Science

MICHIGAN TECHNOLOGICAL UNIVERSITY

2009

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This dissertation, “The Influence of Concurrent Disturbances on Plant Community Dynamics in Northern Hemlock-Hardwood Forests” is hereby approved in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the field of Forest Science.

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PREFACE

This dissertation includes findings from four unique studies that are presented as four individual chapters. One of these chapters was submitted as a manuscript for peer-reviewed publication. This chapter and the current manuscript status are acknowledged by a foot note in the text.

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ABSTRACT

Throughout the Upper Great Lakes region, alterations to historic disturbance regimes have influenced plant community dynamics in hemlock-hardwood forests. Several important mesic forest species, eastern hemlock (*Tsuga canadensis*), yellow birch (*Betula alleghaniensis*), eastern white pine (*Pinus strobus*), and Canada yew (*Taxus canadensis*), are in decline due to exploitive logging practices used at the turn of the 20th century and the wave of intense fires that followed. Continued regeneration and recruitment failure is attributed to contemporary forest management practices and overbrowsing by white-tailed deer (*Odocoileus virginianus*). Therefore, I examined the influence of two concurrent disturbances, overstory removal and herbivory, on plant community dynamics in two hemlock-hardwood forests. I measured the post-disturbance regeneration response (herbaceous and woody species) inside and outside of deer exclosures in 20 artificial canopy gaps (50 – 450 m²) and monitored survival and growth for hundreds of planted seedlings.

The results of this research show that interacting disturbances can play a large role in shaping plant community composition and structure in hemlock-hardwood forests. White-tailed deer herbivory homogenized the post-disturbance plant communities across the experimental gradient of gap areas, essentially making species compositions in small gaps “look like” those in large gaps. Deer browsing also influenced probability of survival for planted Canada yew cuttings; all else being equal an individual was nearly seven times more likely to survive if protected from herbivory ($P < 0.001$). In contrast, the ability of sugar maple (*Acer saccharum*) to persist under high levels of herbivory and respond rapidly to overstory release appears to be related to the presence of stem layering

(i.e., portions of below-ground prostrate stem). Layering occurred in 52% of excavated saplings ($n = 100$) and was significantly associated with increased post-disturbance height growth. Understory light was also important to planted seedling establishment and height growth. Higher levels of direct under-canopy light negatively impacted survival for shade-tolerant hemlock and Canada yew, while an increase in diffuse light was linked to a higher probability of survival for yellow birch and height growth for hemlock and Canada yew. Increases in white pine height growth were also significantly associated with a decrease in canopy cover.

INTRODUCTION

Worldwide, forest ecosystems are experiencing dramatic and rapid changes. Habitat fragmentation, timber harvesting, and the introduction of exotic pests and pathogens are disrupting natural disturbance regimes (Mayer and Rietkerk 2004). For forest ecosystems, the frequency, size, severity, and interactions among disturbances determine successional trajectories (Frelich 2002). Therefore, modification of disturbance regimes not only affects tree seedling establishment and recruitment, but ultimately changes the composition and structure of forests (Frelich 2002).

Disturbance in hemlock-hardwood forests

Throughout the Upper Great Lakes region, alterations to historic disturbance regimes have hindered the natural regeneration and recruitment of several important mesic forest species. Eastern hemlock (*Tsuga canadensis* (L.) Carr.), yellow birch (*Betula alleghaniensis* Britton), eastern white pine (*Pinus strobus* L.), and Canada yew (*Taxus canadensis* Marsh.) have all experienced declines in abundance post European settlement. Historically, these species were major components of the northern hemlock-hardwood community, in which they prevailed on cool and moist upland sites (Abrams 2001; Martell 1974; Rooney 2000). Fire, wind, and herbivory interacted to shape the characteristics of these forests (Frelich, 2002). Since the late 1800s, wide-scale logging coupled with intense slash fires (late 1800s and early 1900s), increased herbivory by white-tailed deer (*Odocoileus virginiana* Zimmermann), and contemporary fire suppression have favored the establishment of other tree species, such as sugar maple (*Acer saccharum* Marsh.) and aspen (*Populus* spp.), over hemlock, yellow birch, and

white pine (Frelich 1995; Godman and Krefting 1960; Mladenoff and Stearns 1993; Rooney 2000; Weyenberg et al. 2004). Intensive ungulate browsing is the primary contributor to the decline of Canada yew (Martell 1974).

Logging reached peak levels in the Great Lakes region in the late 1800s and early 1900s (Whitney 1987). For a time, harvesting was selective for white pine. Then as that species became scarce, the focus shifted to hemlock and later to hardwoods (Whitney 1987). Logging not only changed forest species composition, it created new habitats for white-tailed deer. Deer were scarce in the pre-settlement forests of the Upper Peninsula of Michigan, which is located at the northern edge of the species' range (Van Deelen et al. 1996). The large expanses of primary forest (i.e., not previously harvested) that occupied the region at the time lacked the undergrowth required to support large deer populations (Alverson et al. 1988). When commercial logging was introduced to the area in the 1880s, deer responded favorably due to the increase in browse, which in turn increased their summer range northward (Frelich and Lorimer 1985). Logging provided deer with browse both through the slash (tree tops, etc.) that was left behind and the natural regeneration that followed (Stoeckeler et al. 1957). Since logging operations began, deer populations have been consistently higher than pre-settlement populations, excluding the 40-year period (approximately 1880 – 1920) when widespread logging-slash fires destroyed most of the suitable habitat that was made available to deer (Frelich and Lorimer 1985). After 1920, effective fire management programs allowed large areas of hardwood forests to reestablish. White-tailed deer populations have remained relatively high ever since (Frelich and Lorimer 1985). As a result, elevated white-tailed deer densities and their effects on forest ecosystems have become major concerns in the

Great Lakes region. Several studies have documented the decline in forest plant diversity (as reviewed by Rooney 2001; and Cote 2004) and the reduction in regeneration of several tree species (Alverson et al. 1988; Rooney and Waller 2003) due to deer browsing.

Dissertation overview

My goal for this dissertation work was to determine how multiple disturbances influence plant community dynamics in northern hemlock-hardwood forests and how these interactions, in turn, affect mesic forest species regeneration. I examined natural and artificial regeneration (i.e., planted seedlings) across a range of environmental conditions and under varying levels of white-tailed deer herbivory for five mesic forest tree and shrub species: eastern hemlock, eastern white pine, Canada yew, yellow birch and sugar maple. This body of work addresses three overarching questions: (1) how do concurrent disturbances, such as overstory removal and white-tailed deer herbivory, interact to influence forest plant community dynamics? (2) In post-disturbance environments, what factors are the most influential to seedling establishment and early growth? (3) For mesic forest species that dominate under contemporary disturbance regimes (e.g., sugar maple), what characteristics allow for persistence while other species face rapid decline (as discussed above)?

Chapter one describes the results of a controlled experiment designed to test the influences of understory light levels and white-tailed deer herbivory on the mesic shrub species Canada yew. Over 1,000 stem cuttings were planted in a hemlock-hardwood forest at Michigan Technological University's Ford Forestry Center, on the edges of 10

artificial gaps (61 - 441 m²) and under closed-canopy conditions. Half of the cuttings were planted inside deer exclosures. I monitored survival and growth for four years and tested the following three hypotheses: (1) elevated understory light levels will increase *T. canadensis* growth; (2) subsequently, higher growth rates will decrease the impact of biomass loss to herbivores and increase long-term survival; and, (3) the initial vigor of an individual at the time of planting will also be indicative of its ability to survive, grow, and withstand herbivore damage.

Chapter two explores how post-disturbance plant community composition (both woody and herbaceous species) is influenced by scale of overstory disturbance and white-tailed deer herbivory. I measured vegetation response inside and outside deer exclosures in 20 artificial canopy gaps (50 – 450 m²) installed in the same hemlock-hardwood forest as described above to test the following two hypotheses: (1) herbivory will influence ground-layer community response to gap formation by shifting species compositions and (2) these shifts will either be (a) more pronounced in large gaps due to increased browse availability (i.e., large gaps would be more attractive to deer than small gaps) or (b) more distinct in small gaps because of the higher probability of individual plant mortality from ungulate browsing (i.e., small gaps have less browse available).

In chapter three I discuss how stem layering may be an adaptive trait that allows sugar maple to respond rapidly to release following disturbance, even under high rates of herbivory. Previous work by others suggests that layering (i.e., prostrate stem sections that develop adventitious roots after being buried by leaf litter) may be an important adaptive trait that allows advance regeneration to stay small and grow older while suppressed in the understory (Hibbs and Fisher 1979; Woods 2008). To test the influence

of stem layering on the response of sugar maple to release in canopy openings, I excavated 100 sugar maple saplings from both exclosure and control plots to determine the influence of browsing and gap light environment on sapling growth rates, tissue quality, and biomass allocation. I hypothesized that stem layering would provide a competitive advantage that would allow sugar maple to tolerate higher levels of stress associated with herbivory by deer.

Finally, Chapter 4 examines the factors that influenced early survival and growth (3-year) for three mesic forest species (~900 seedlings) underplanted in a recently harvested northern hardwood forest located on the Keweenaw Peninsula of Michigan. My goal for this study was to examine the effectiveness of underplanting for restoring yellow birch, eastern white pine, and eastern hemlock to degraded northern hardwood forest communities. The study objectives were (1) to identify microsite characteristics that favored or harmed planted seedling establishment and growth and (2) to determine if neighborhood competition influences planting success.

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CHAPTER ONE

Death and *Taxus*: the High Cost of Palatability for a Declining Evergreen Shrub, *Taxus canadensis*¹

Abstract

Taxus canadensis Marsh., a shade-tolerant, evergreen shrub, is in decline due to past anthropogenic disturbances and increased cervid browsing. To identify factors that may be influencing establishment for this species, we planted 1,080 *T. canadensis* cuttings in a hemlock-hardwood forest in the spring of 2004. Cuttings were planted across a gradient of light environments, artificial canopy gaps (61 - 441 m²) and closed canopy conditions, and half were protected with deer exclosures. Following four growing seasons, *T. canadensis* survival in exclosures was 92% compared with 75% in controls. A mixed-effects binary logistic regression analysis revealed that deer exclusion had the most influence on probability of survival; all else being equal an individual was nearly seven times more likely to survive if planted inside an exclosure ($P < 0.001$). Increasing light intensity had a counterbalancing effect on growth and survival; light increased leader growth ($P = 0.019$), but reduced an individual's probability of survival ($P < 0.001$), possibly due to enhanced herbivory and elevated moisture stress. Consequently, enhancing resource availability and growth may not decrease the impact of biomass loss to herbivory. These results suggest that even with relatively low herbivore densities, exclosures are required for the recovery of highly palatable species.

¹This chapter has been accepted as a manuscript by Holmes, S.A., Webster, C.R., Flaspohler, D.J., and Froese, R.E. for publication pending minor revisions at Canadian Journal of Forest Research.

Introduction

In forest ecosystems, woody shrubs face many challenges in the struggle for survival and growth. In addition to coping with the high shade environment of the forest floor (Oliver and Larson 1996), in many systems, shrubs have to contend with the presence of mammalian herbivores. Since these understory inhabitants spend their entire existence within the reach of browsers, they must carefully balance the allocation of limited resources between maintenance, growth, and defense (Herms and Mattson 1992). When nutrients and light are readily available, fast-growing species rapidly re-grow tissues to compensate for herbivore consumption, but if resources are limited, investment in defense may be the preferred option (Augustine and McNaughton 1998). The production of anti-herbivore defenses is advantageous only when the benefits of protection exceed costs (Coley et al. 1985). Therefore, for species with slow foliar turnover rates, such as understory evergreen shrubs, the protection of existing leaves may be more cost effective than simply growing new ones (Coley and Barone 1996; Coley et al. 1985).

With time, herbivore damage can select for (constitutive resistance) or stimulate (induced resistance) protective mechanisms (Strauss et al. 2002) in plants to deter or reduce further herbivore damage. Defenses range from chemical compounds that make foliage toxic or unpalatable (rev. by Augustine and McNaughton 1998; Hobbs 1996) to mechanical structures that dissuade browsers (e.g., thorns; Gomez and Zamora 2002). For example, in Japan the temperate, evergreen shrub *Damnacanthus indicus* C. F. Gaertn., exhibits shorter leaf lengths, thicker spines, and smaller internode distances between spines in regions with Sika deer (*Cervus nippon* Temminck) compared to those without

(Takada et al. 2001). Some understory shrubs, however, such as the conifer, *Taxus canadensis* Marsh., commonly known as Canada yew or ground hemlock, appear to lack any apparent resistance to ungulate browsers. Despite the presence of the toxin paclitaxel in its foliage (Senneville et al. 2001), this shrub is favored browse for white-tailed deer (*Odocoileus virginiana* Zimmermann) in winter and for moose (*Alces alces americana* Clinton) year-round (Martell 1974).

Several authors (Alverson et al. 1988; Jenkins and Bartlett 1959; Leopold et al. 1947; Martell 1974; Telfer 2004) provide observational evidence to link the decline of *T. canadensis* throughout its natural range, which includes the Midwest and Northeast regions of the United States and southeastern Canada (Martell 1974), to over browsing by white-tailed deer, but experimental data are uncommon. Historically, this species was common to cool and moist sites, including maritime provenances of the Lake States, until extirpated from many areas with high deer populations (Martell 1974). Undoubtedly, widescale logging and subsequent fires that were prevalent at the turn of the last century have also contributed to the decrease in abundance (Jensen 1943; Whitney 1994). Today this species is largely associated with primary and old-growth forests (Stachowicz and Allison 1995; Tyrrell and Crow 1989), sites which typically escaped fires, and areas with high winter snowfall where deer densities are low (Doepker, 1995). It has also been associated with some mid-successional forests that are dominated by *Quercus rubra* L. and *Acer rubrum* L. (Stachowicz and Allison 1995). In addition, once a plant's population is reduced, accelerated rates of extirpation by deer can occur (Côté et al. 2004). This implies that deer may not only be influencing established populations; they may also be hindering the establishment and recruitment of new individuals dispersing

outside these current population zones. While studies have looked at the direct impacts of deer browsing on existing *T. canadensis* populations (Allison 1990a, b, 1992; Beals et al. 1960; Stachowicz and Allison 1995) to our knowledge, none have evaluated the biological or environmental factors that influence the survival and growth of newly established individuals. Restoration of *T. canadensis* is desirable; in addition to contributing to forest understory diversity and structure, this species provides habitat for shrub nesting song-birds and small mammals (Belant and Windels 2003). Its arils are also eaten by both birds and rodents (Wilson et al. 1996).

To identify environmental factors that may influence survival and growth for a highly palatable, understory shrub species, we planted 1,080 *T. canadensis* cuttings in a hemlock-hardwood forest in the western Upper Peninsula of Michigan. We planted cuttings inside and outside of deer exclosures located on the edges of artificial canopy gaps and under closed canopy conditions. Our experimental design provided a gradient of understory light levels for *T. canadensis* growth and allowed us to directly test the impact of herbivory under a variety of environmental conditions. We tested the following hypotheses: (1) elevated understory light levels will increase *T. canadensis* growth; (2) subsequently, higher growth rates will decrease the impact of biomass loss to herbivores and increase long-term survival; and, (3) the initial vigor of an individual at the time of planting will also be indicative of its ability to survive, grow, and withstand herbivore damage.

Materials and Methods

Study site

This *T. canadensis* planting experiment was conducted in a hemlock-hardwood forest located at Michigan Technological University's Ford Forestry Center (46°37'N 88°29'W) near Alberta, Michigan. Alberta is situated in the western portion of Michigan's Upper Peninsula. Soils in our study gaps were dominated by moderately well drained Kallio cobbly silt loams, 1 – 20% slopes, with small areas of poorly drained Pickford mucky silt loams in depressions (Berndt 1988). Mean winter and summer temperatures are -9.8° C and 17.4° C, respectively (Berndt 1988). Total mean annual precipitation is 87.4 cm and mean winter snowfall is 382.5 cm (Berndt 1988). Deer densities for the region range from 6.5 deer km⁻² in the spring to 9.3 deer km⁻² in the fall (Mayhew 2003). Given the spatial extent of the study area, approximately 60 ha, it is unlikely that deer densities varied substantially across the study site.

Study design and data collection

Rooted stem cuttings of *T. canadensis* were planted in the last two weeks of June 2004, on the edges of artificial canopy gaps and under closed canopy conditions. Cuttings were grown at the J. W. Toumey Nursery and were fertilized and hardened off prior to planting. Artificial canopy gaps were created in hemlock stands during the winter of 2002 – 2003 through the removal of low quality hardwoods. In total, 21 gaps were installed and were categorized as small, medium, and large: 50 - 150 m², 151- 250 m², and 251- 450 m², respectively. Of these, three small, four medium, and three large gaps were randomly chosen for *T. canadensis* planting. Cuttings were planted in four arrays within

each gap; arrays contained four, 1- m² plots, two of which were randomly chosen for deer exclosures and were located at the north, east, south, and west edges of each gap (Fig. 1-1). In addition, five randomly placed, closed canopy arrays, hereafter referred to as null gaps, were also established for comparison. Each null gap contains four, 1- m² plots, two of which were randomly chosen for deer exclosures. Our mini-hoop deer exclosures (1 m radius, 1.52 m high) were constructed from heavy gauge, 15 cm² wire mesh. This mesh size excludes white-tailed deer, but not snowshoe hare (*Lepus americanus* Macfarlane). We planted six *T. canadensis* cuttings within each plot for a total of 1,080 cuttings. All individuals were watered for the first two weeks following planting.

At the time of planting (June 2004), the initial condition of each yew cutting was documented. Leader length, hereafter referred to as height, and stem diameter, measured at ground level with digital calipers, were recorded (Table 1-1) along with the initial vigor of each plant. Height was determined by outstretching the dominant leader and measuring the distance between its terminal and the plant's base. Each cutting's vigor was visually assessed and assigned to one of three categories: fair, good, or excellent (Fig. 1-2). Several attributes were considered for assigning vigor class: diameter, height, foliage color and density, and amount of branching. Pearson's chi-square test verified that individuals in the three vigor classes were evenly distributed between control and exclosure treatments (Fig. 1-3) at the time of planting ($\chi^2 = 0.282$, df = 2, $P = 0.868$).

Taxus canadensis survival was tallied after two, three, and four growing seasons.

In September of 2007, we re-measured the height and diameter of each individual and visually estimated the percent cover of competing vegetation by functional group (graminoids, ferns, club moss, *Equisetum* spp., forbs, woody, and *Rubus* spp.) for each

plot (Table 1-1). In order to quantify the understory light environment at each plot, we took a digital hemispherical photograph 70 cm above the center of each plot. When combined with spatial location, percent slope, and aspect, hemispherical photography can be used to model local light availability at various points within a given canopy gap (WinScanopy 2005). Digital hemispherical photographs were analyzed with the software WinSCANOPY (WinScanopy 2005) to determine the levels of direct and diffuse below canopy radiation for each plot. This was measured as the mean direct and diffuse photosynthetically active flux density for the growing season ($\text{mol m}^{-2} \text{day}^{-1}$; Table 1-1). WinSCANOPY's default growing season period was used, which is May 1 – September 30.

Data analysis

Our experimental design had a hierarchical structure; yew cuttings were planted in arrays, and arrays were clustered within artificial canopy gaps. This did not allow us to assume independence between individual *T. canadensis* cuttings growing within the same spatial unit (arrays or gaps). Therefore, we used mixed-effects statistical methods that accounted for this hierarchical structure in our data (Schabenberger and Pierce 2002).

Binary logistic regression models with mixed-effects, implemented in the statistical environment R (R Development Core Team 2008), were used to identify *T. canadensis* cutting and environmental variables that best predict survival ($n = 1,080$) after four growing seasons. We also explored dimensional changes in *T. canadensis* with multiple linear mixed-effects regression models in the same statistical environment. We calculated relative change in height and as the percent change in height between the

initial height measurement (June 2004) and the final height measurement (September 2007). Absolute change in height was calculated by subtracting the initial height measurement (June 2004) from the final height measurement (September 2007). These methods were also used to calculate diameter change. First, we sought to determine the influence of treatment on dimensional change for all surviving individuals ($n = 857$). Then we explored the influence of environmental variables and initial *T. canadensis* size on the height growth of extant individuals that escaped herbivory in exclosures ($n = 445$). For the later two height models, we used a square root transformation to normalize the response variable.

Both types of methods, binary logistic regression with mixed-effects and multiple linear mixed-effects regression, were used to analyze the effect of initial cutting characteristics and environmental variables (fixed effects) on the response variable (survival and height growth, respectively) while fitting a nested random effect to each array and gap. The random effect accounts for the spatial correlation within arrays and gaps and the variation between arrays and gaps (Schabenberger and Pierce 2002). For all three models (survival, relative height growth, and absolute height growth), we first fitted a full model, which included as fixed effects the initial dimensions of *T. canadensis*, environmental variables (see Table 1-1), and associated interaction terms, and random effects for gap and array. We then tested the significance of the random effects, after which, non-significant fixed effects were removed one at a time until only significant terms remained. Non-significance was further verified by re-addition of the removed variables to the reduced model. Akaike's Information Criterion (AIC) and Akaike weights were used to select the most parsimonious and biologically meaningful models and

likelihood ratio tests were used to assess statistical significance. Finally, we calculated a generalized R^2 following the procedure outlined by Nagelkerke (1991).

Results

Taxus canadensis survival was significantly associated with deer exclusion. After four growing seasons, 91.9% of individuals in exclosures ($n = 540$) were alive, compared to just 75.0% of cuttings planted in control plots ($n = 540$). Most of the surviving control plot cuttings were in poor condition as discussed below. The survival model (Table 1-2) revealed that the presence of an exclosure had the most influence on *T. canadensis* survival. All else being equal, an individual was 6.61 times more likely to survive if it was planted within an exclosure (Table 1-2). In addition to treatment, the model also revealed that light environment, competition, and vigor class were associated with survival (Table 1-2). Higher levels of under-canopy direct radiation reduced an individual's probability of survival, mean (\pm SD) direct radiation for survivors ($n = 857$) and non-survivors ($n = 223$) was $9.24 \pm 4.49 \text{ mol m}^{-2} \text{ day}^{-1}$ and $11.14 \pm 5.12 \text{ mol m}^{-2} \text{ day}^{-1}$, respectively, while higher levels of forb and fern coverage increased it. An initial vigor classification of fair reduced an individual's chance of survival in comparison to good vigor, and excellent vigor increased it (Table 1-2).

The presence of exclosures greatly reduced the amount of herbivore damage on cuttings in treatment plots. In 2007, 93.9% of all control plot individuals were browsed compared to just 3.8% of *T. canadensis* planted in exclosures. Damage in the exclosure plots was attributed to snowshoe hare. Although initial heights and diameters of *T. canadensis* cuttings planted in control and exclosure plots were very similar (Table 1-1),

after four growing seasons large differences in height and diameter growth between the two treatments were observed. Diameters increased for almost all of the surviving individuals (Fig. 1-4) regardless of treatment, but the increases were greater in exclosures ($n = 857$, $df = 811$, $t = 12.97$, $P < 0.001$). While *T. canadensis* cuttings planted within exclosures increased in height, change in height was negative for almost all of the individuals within control plots (Fig. 1-5a and 1-5b); relative height change and absolute height change varied significantly between exclosure and control plots for surviving individuals ($n = 857$; $t = 26.61$, $df = 811$, $P < 0.001$ and $t = 28.80$, $df = 811$, $P < 0.001$, respectively). Given the reduced condition of control plot individuals, we expect that mortality will increase with time since high rates of browsing are likely to continue.

For individuals surviving inside of exclosures with no evidence of browse damage ($n = 445$), both relative and absolute change in height over four growing seasons could be predicted by initial *T. canadensis* dimensions and diffuse under-canopy radiation, which ranged from 0.86 to 2.14 mol m⁻² day⁻¹ (Table 1-3). Taller initial heights ($P < 0.001$) decreased relative change in height growth, while larger initial diameters ($P = 0.031$) and higher levels of diffuse under-canopy radiation ($P = 0.047$) increased it (LRT = 96.21, $P < 0.001$, $R^2 = 0.19$; Table 1-3). Absolute height growth over four growing seasons was also associated with larger initial diameters and higher levels of diffuse under-canopy radiation ($P = 0.007$ and 0.019, respectively), which explained 10% of the variation (LRT = 46.89, $P < 0.001$, $R^2 = 0.10$; Table 1-3). Initial height was not a significant variable ($P = 0.370$) in the absolute height growth model.

Arils, which are the red, fleshy berry-like reproductive structures that encase single seeds (Soper and Heimburger 1982), were observed on five exclosed *T.*

canadensis, but none were found on control plot plants. Mean aril production was 1.2 (\pm 0.4 SD) arils/plant. Four of these individuals were growing in the southern array of a small gap (96 m²). The fifth individual was located on the eastern edge of a medium gap (174 m²). Mean height and diameter of the aril producing *T. canadensis* were 33.2 (\pm 9.8 SD) cm and 4.5 (\pm 0.7 SD) mm, respectively.

Discussion

In some plant communities, ungulate abundance and overall browsing intensity may be poor predictors of individual species response as a result of contemporary community composition or discontinuities between historic and contemporary ungulate density or habitat associations. In northwestern Pennsylvania, where presettlement deer densities are estimated to be 3 - 4 deer km⁻², forest herb and shrub species have been negatively impacted at densities as low as 3.7 deer km⁻² and lost outright at densities exceeding 7.9 deer km⁻² (as rev. by deCalesta 1997). These densities are much lower than those reported for other locations where ground-layer communities are experiencing deer induced changes, for example, deer densities reached 43 deer km⁻² in the 1970's in Cades Cove, Great Smoky Mountain National Park (Griggs et al. 2006). What may appear to be low, however, may still be well in excess of historic levels; deer densities in the western portion of Michigan's Upper Peninsula are twice as high as they were prior to European settlement (Doepker et al. 1995). Deer populations are considered "overabundant" when they alter ecosystem function or decrease the densities of desired species, but this value-laden term must be considered in context (McShea et al. 1997). Plant species vary greatly in their tolerance for deer herbivory. Therefore, systems that appear to be at low risk for

over browsing due to relatively low ungulate populations may still be susceptible to damage. In addition, once a plant species becomes rare, even large reductions in deer densities may not facilitate recovery (Balgooyen and Waller 1995; Coomes et al. 2003). For some plant communities, the discontinuity between historical and current densities of plant species and deer may be more important for assessing herbivory risk than actual deer density numbers.

Our results indicate that the ability of *T. canadensis* to persist on the landscape may be threatened by contemporary levels of deer herbivory and the establishment of new populations in areas with even moderate deer densities will not be possible without deer exclusion. The high palatability of *T. canadensis* and low tolerance to browsing suggest that this species may have evolved in the absence of large deer populations; it seems to lack any defense mechanisms to deal with present levels of deer herbivory. At our study site, where deer densities are relatively low, ranging from 6.5 deer km⁻² in the spring to 9.3 deer km⁻² in the fall, compared to other regions in the western Upper Peninsula of Michigan (Mayhew 2003), only 75% of control plot individuals survived after four years and almost 94% of control plot cuttings were browsed. This resulted in a significant reduction in leader length over the course of our study, and left surviving individuals in poor condition. Our results are consistent with the work of Beals et al. (1960) in the Apostle Islands of Lake Superior. They found that *T. canadensis* was highly susceptible to deer browse damage and even moderate browse pressure resulted in decreased densities. Since the existence of high density white-tailed deer populations throughout the range of *T. canadensis* appears to be a rather recent occurrence, within the last century (rev. by Côté et al. 2004; see also Whitney 1994), the wide scale distribution

and abundance of this species in the past (Martell 1974) coupled with low deer densities may have allowed *T. canadensis* to tolerate high rates of localized browsing.

Remnant *T. canadensis* populations, on the other hand, may not be able to cope with the detrimental effects of deer herbivory. Even in an area with comparatively low deer densities, the enhancement of resources for growth did not appear to dampen the impacts of browsing as we had initially hypothesized. Although our height change models suggest that increased diffuse light levels increase the rate of height growth, survival was negatively correlated with direct under-canopy radiation. Although gaps increase the availability of diffuse light, they also increase the daily duration of direct sunlight hitting the forest floor (Paquette et al. 2007). *Taxus canadensis* is typically found in damp and shaded environments (Soper and Heimburger 1982) and is extremely shade-tolerant (Martell 1974); therefore, the elevated, gap edge radiation levels (Canham et al. 1990) may be harmful. In addition, the drier conditions found along the well illuminated northern edges of gaps (Wright et al. 1998) may have a negative effect on growth. In New Hampshire, Stachowicz and Allison (1995) found that the natural distribution of *T. canadensis* was associated with concave, north- and east-facing slopes; conditions that result in lower solar radiation and higher soil moisture levels. In addition, north-facing slopes tended to produce the most *T. canadensis* biomass (Stachowicz and Allison 1995). Biomass production was also somewhat higher in deciduous forests versus coniferous forests, but the former forest type exhibited higher biomass losses to white-tailed deer browsing (Stachowicz and Allison 1995). Since higher levels of forb and fern coverage increased the probability of *T. canadensis* survival (all else being equal) in our planting, we suggest that these functional groups provide visual protection from deer and/or their

shade enhances soil moisture for growth. Garcia et al. (2000) found that fleshy-fruited shrubs protected seedlings of another yew species, *Taxus baccata* L., from herbivory and summer drought in the Sierra Nevada and provided microhabitats for the successful establishment of new seedlings.

We found moderate support for our third hypothesis since the initial condition of a *T. canadensis* cutting was indicative of its capacity for four-year survival and height growth, but not to produce reproductive structures. Individuals whose vigor classifications were excellent at the time of planting were more likely to survive than good or fair individuals (Table 1-2), and large initial diameters were positively associated with four-year height change (relative and absolute; Table 1-3). Initial height, however, was associated with reduced four-year relative height change, but was not a significant predictor of absolute height change (Table 1-3). None of the excellent vigor individuals produced arils; three out of five aril-producing *T. canadensis* had an initial vigor of good, while the other two were initially classified as fair. To our knowledge, the arils we observed in the fall of 2007 mark the first year of aril production since the time of planting.

Deer herbivory may also be impacting sexual reproduction of *T. canadensis*. In our study, only protected cuttings produced arils. In a comparative study of natural *T. canadensis* populations in the Apostle Islands, Allison (1990a) found that increased levels of deer browsing damage were correlated with lower male strobuli, ovule, and seed production. An enclosure study in the same system also revealed that protected *T. canadensis* produced more male and female strobuli than individuals outside of enclosures, but significant differences were not seen until the fourth year of protection

(Allison 1990a). Although sexual reproduction is important for the exchange of genetic material, this species appears to maintain its populations locally through vegetative propagation rather than seed dispersal (Senneville et al. 2001). *Taxus canadensis* reproduces vegetatively through layering (Allison 1990a); therefore, it is likely that this process is also being negatively impacted by deer. Other clonal woody shrubs have exhibited negative responses to mammalian herbivory. Zeigenfuss et al. (2002) reported that elk (*Cervus elaphus* L.) browsing significantly reduced vegetative production for clonal willow species (*Salix* spp.) in Rocky Mountain National Park (Colorado, USA). Likewise, Wang et al. (2007) found that giant panda (*Ailuropoda melanoleuca* David) herbivory reduced new shoot densities for the clonal shrub *Fargesia qinlingensis* Yi et J.X. Shao (arrow bamboo) in China.

In conclusion, it seems that lack of defenses in *T. canadensis* against white-tailed deer herbivory will prevent its recovery in areas with even low to moderate deer densities. Its high palatability exceeds even that of *Tsuga canadensis* (L.) Carr. and *Thuja occidentalis* L. (Beals et al. 1960; Leopold et al. 1947), two species documented as experiencing widespread recruitment failure due to white-tailed deer (Anderson and Loucks 1979; Frelich and Lorimer 1985; Rooney and Waller 2003). Unlike these tree species, though, *T. canadensis* can never escape the white-tailed deer browse zone through height growth after it is established. The plight of this species raises an important ecological question: how do highly palatable species cope with demographic change? With deer populations on the rise throughout Europe and North America (Côté et al. 2004), the impact of population shifts on plant-herbivore interactions clearly warrants further investigation and a more proactive approach to plant conservation.

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Table 1-1 Environmental attributes of sample plots and initial dimensions of *Taxus canadensis* cuttings.

	<i>Taxus canadensis</i> ^a		Understory Light ^{b,c}			Competition Percent Cover by Functional Group ^b						
	Height (cm)	Diameter (mm)	Direct	Diffuse	Total	Forbs	Graminoids	Woody	<i>Rubus</i>	Fern	Fern Allies ^d	Total
<i>Control</i>												
Mean	16.4	2.3	9.7	1.4	11.1	7.7	9.4	6.8	2.7	5.1	0.6	32.2
Median	16.0	2.2	8.5	1.4	9.9	4.0	1.5	4.0	0.0	0.0	0.0	19.0
Min	5.0	0.7	1.7	0.7	3.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Max	40.0	4.9	23.3	2.2	25.1	85.0	100.0	54.0	55.0	48.0	10.0	148.0
SD	4.9	0.7	4.8	0.2	4.8	12.3	20.5	8.2	9.8	8.6	1.6	35.2
<i>Exclosure</i>												
Mean	16.3	2.3	9.6	1.4	11.0	10.1	4.8	10.0	4.2	7.8	1.3	38.1
Median	16.0	2.2	9.0	1.4	10.3	6.5	1.0	6.5	0.0	2.0	0.0	26.8
Min	5.0	0.8	1.5	0.9	2.5	0.0	0.0	0.0	0.0	0.0	0.0	1.5
Max	40.0	5.2	23.3	2.1	23.6	50.0	52.0	54.0	95.0	70.0	50.0	153.0
SD	4.6	0.7	4.6	0.2	4.7	10.0	8.6	10.7	15.5	13.3	5.7	34.7

^aInitial dimensions measured in 2004, n = 1080.^bMeasured in 2007 for each subplot (n = 180). Descriptive statistics were calculated for control plots (n = 90) and exclosure plots (n = 90).^cDirect and diffuse below canopy radiation: photosynthetically active flux density under-canopy average for the growing season (mol m⁻² day⁻¹) (WinSCANOPY, 2005).^dFern allies include club mosses and *Equisetum* spp.

Table 1-2 Binary logistic regression model using mixed-effects to analyze the influence of environmental factors on probability of *Taxus canadensis* survival (live = 1, zero otherwise).

<i>Survival Model</i>						
Fixed Effect	Estimate	SE	P value	Odds Ratio		
				Estimate	95% CI	
Intercept	1.39	0.35	<0.001			
Exclosure	1.89	0.21	<0.001	6.61	4.42	9.88
Vigor (fair v. good)	-1.06	0.21	<0.001	0.35	0.23	0.52
Vigor (excellent v. good)	0.58	0.35	0.088	1.80	0.92	3.55
DirUnd*	-0.08	0.02	<0.001	0.92	0.88	0.97
Forbs	0.02	0.01	0.032	1.02	1.00	1.05
Ferns	0.05	0.02	0.002	1.05	1.02	1.08
<i>Model Fit</i>						
	χ^2	df	P			
Hosmer – Lemeshow	13.23	8	0.104			
Likelihood Ratio	220.07	8	<0.001			

Note: The fixed effects are treatment (exclosure or control), vigor (fair, good, excellent), competition (percent cover forbs and ferns), and light (under-canopy direct radiation). Arrays nested in gaps (45 levels) were treated as the random effect. For the Hosmer - Lemeshow goodness-of-fit test, a significant p-value indicates a lack of model fit.

*Direct under-canopy radiation = photosynthetically active flux density under-canopy average for the growing season ($\text{mol m}^{-2} \text{day}^{-1}$) (WinSCANOPY, 2005).

Table 1-3 Linear mixed-effects models for relative and absolute *Taxus canadensis* height growth (RHG and AHG, respectively) over four growing seasons as a function of initial yew dimensions (height and diameter) and light (DiffUnd; diffuse under-canopy radiation).

Response Variable	Fixed Effect	Estimate	SE	P value	Likelihood Ratio		R ²
					value	P	
sqrt(RHG) ^a	Intercept	8.72	1.23	<0.001	96.21	<0.001	0.19
	DiffUnd ^b (mol m ⁻² day ⁻¹)	1.53	0.77	0.047			
	Initial Height (cm)	-0.24	0.03	<0.001			
	Initial Diameter (mm)	0.52	0.24	0.031			
sqrt(AHG) ^a	Intercept	1.74	0.46	<0.001	46.89	<0.001	0.10
	Initial Diameter (mm)	0.21	0.08	0.007			
	DiffUnd ^b (mol m ⁻² day ⁻¹)	0.69	0.29	0.019			

Note: Arrays nested in gaps (45 levels) were treated as the random effects. Only surviving, unbrowsed, and exclosed cuttings (n = 445) were included in these analyses. The R² applied to the mixed models is a generalization of the classic R² (Nagelkerke, 2001).

^aSquare root transformation used to normalize the response variable.

^bDiffuse under-canopy radiation = photosynthetically active flux density under-canopy average for the growing season (mol m⁻² day⁻¹; WinSCANOPY, 2005).

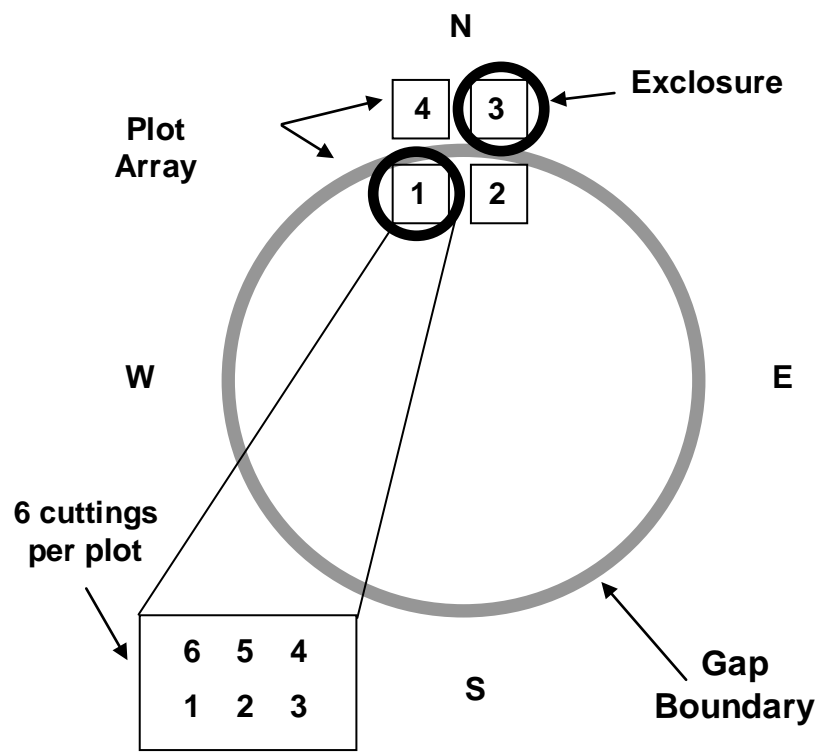


Fig. 1-1 Experimental planting design.



Fig. 1-2 Initial vigor classes for *Taxus canadensis* cuttings (from left to right): fair, good and excellent.

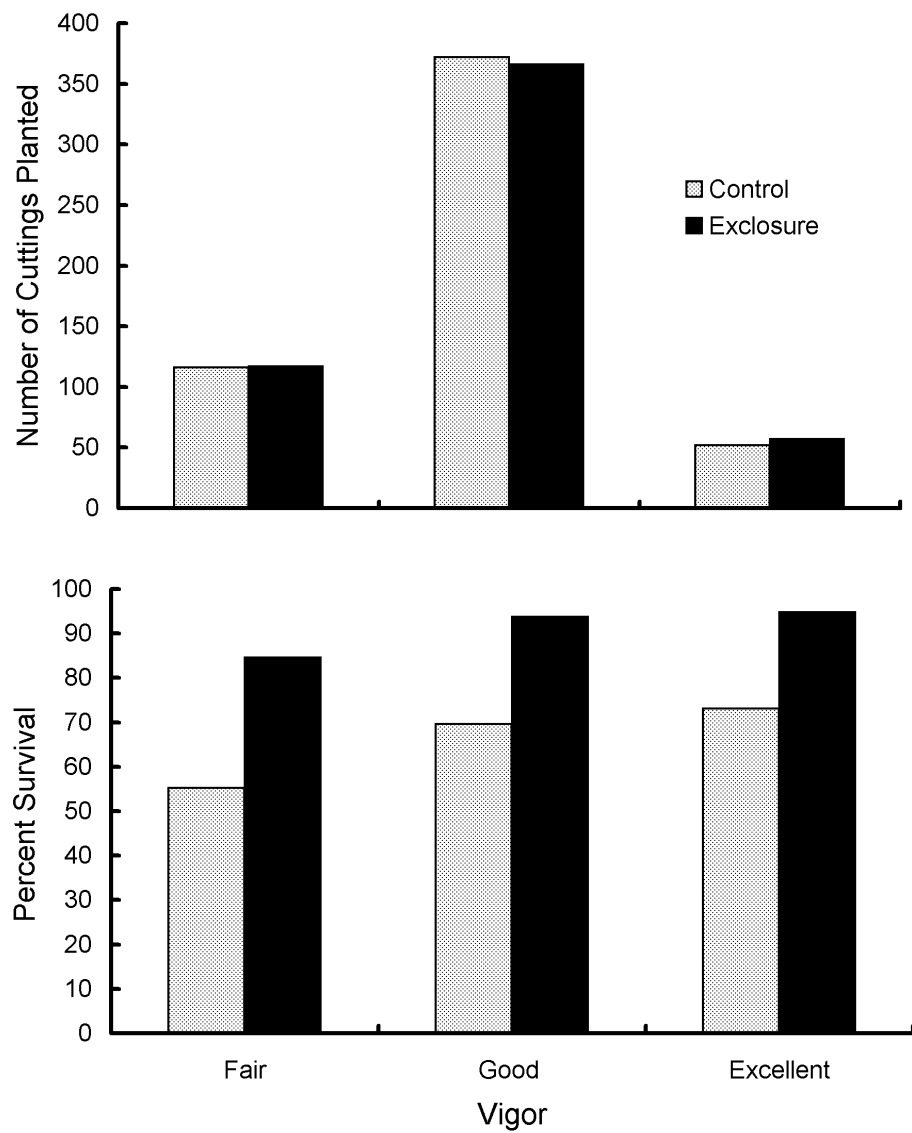


Fig. 1-3 Number of *Taxus canadensis* cuttings (n = 1080) planted in control plots and exclosure plots (a.) and percent survival after four growing seasons (b.) by initial vigor class.

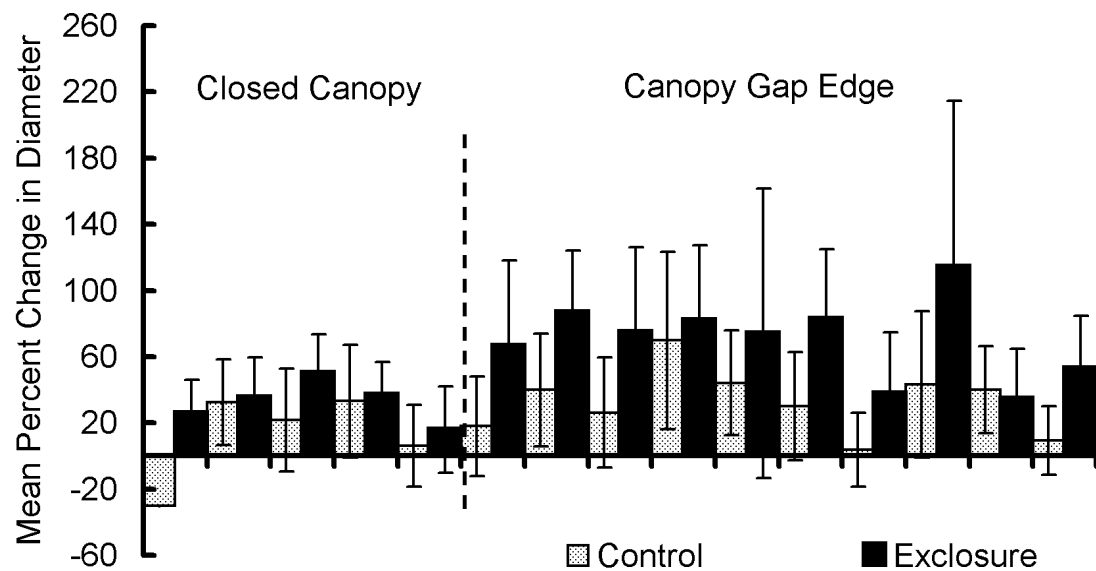


Fig. 1-4 Mean percent change in diameter (± 1 SD) of surviving *Taxus canadensis* after four growing seasons. Each control/exclosure pair represents a single canopy gap or closed canopy array. Study gaps are ordered from smallest to largest along the x-axis. Out of the initial planting of 1080 cuttings, 857 cuttings were still extant following four growing seasons.

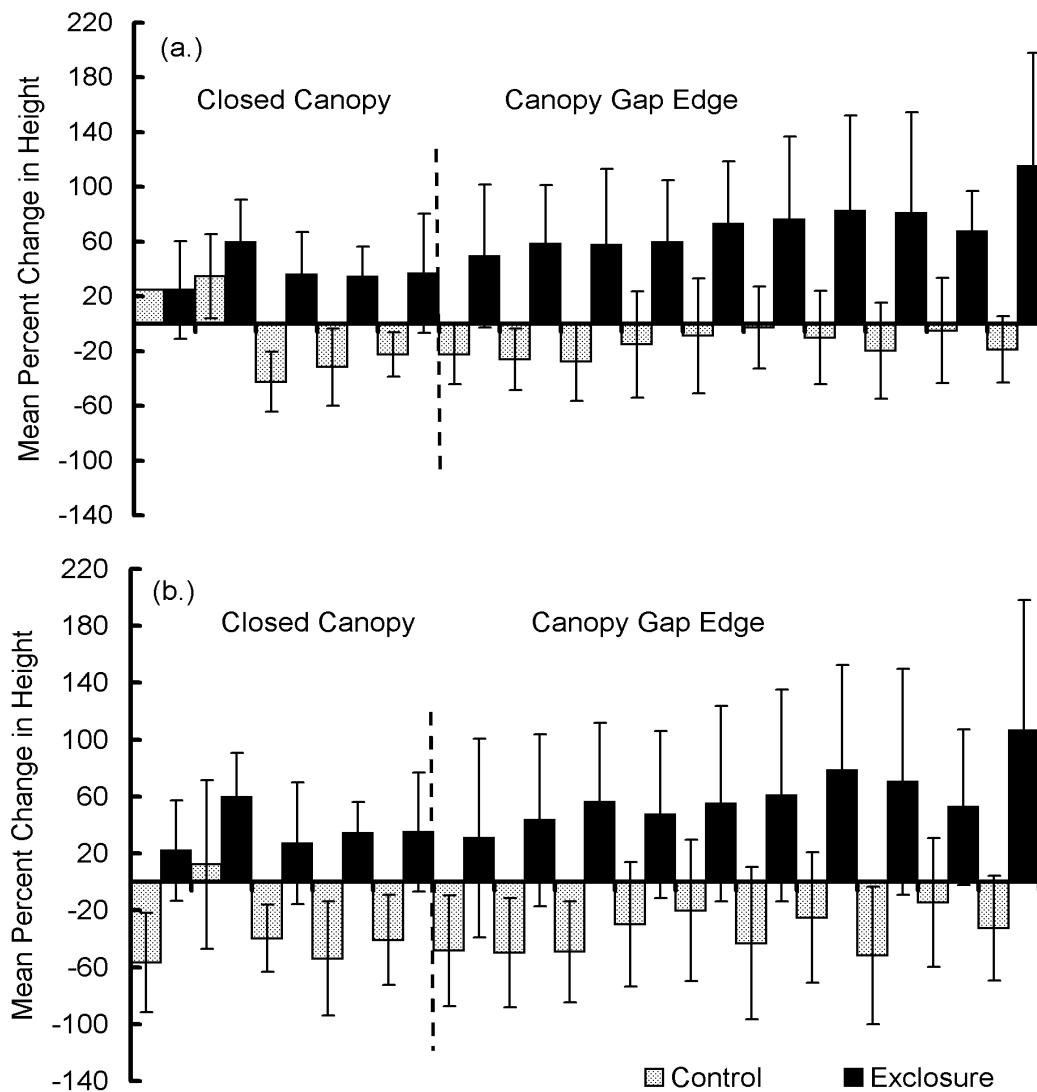


Fig. 1-5 Mean percent change in height (± 1 SD) of *Taxus canadensis* planting following four growing seasons for all *T. canadensis* present (n = 1080), dead and alive (a.), and for all individuals alive (n = 857) four years post-planting (b.). Each control/exclosure pair represents a single canopy gap or closed canopy array. Study gaps are ordered from smallest to largest along the x-axis.

CHAPTER TWO

Herbivore-Induced Expansion of Generalist Species as a Driver of Homogenization in Post-Disturbance Plant Communities

Abstract

1. Disturbance drives ecological change in forest ecosystems. Yet, the interactions between coinciding disturbances, such as overstory removal and herbivory, are not well understood. I used a controlled experiment to investigate how disturbance scale (gap area) influences herbivore foraging behavior. Twenty artificial canopy gaps were installed in a temperate hemlock-hardwood forest: seven small gaps (50 – 150 m²), seven medium gaps (151 – 250 m²), and six large gaps (251 – 450 m²). Within each gap, 4 -12 sample plots were established (depending on initial opening size); 1 - 3 of which were enclosed with 2 m diameter wire mesh deer exclosures.

2. I studied the following interactions: plant community response to canopy removal, response to gap area, and the influence of herbivory on post-disturbance plant communities. I hypothesized that (1) herbivory would shift species compositions (control plot vs. exclosure plot) and (2) these shifts would either (a) be more pronounced in large gaps due to increased browse availability (i.e., large gaps would be more attractive to deer than small gaps) or (b) more distinct in small gaps because of the higher probability of individual plant mortality from ungulate browsing (i.e., small gaps have less browse available).

3. White-tailed deer (*Odocoileus virginianus*) herbivory homogenized the post disturbance plant community across the gradient of gap sizes, essentially making control plot species compositions in small gaps “look like” those in large gaps.
4. Shifts in species composition were attributed to functional group “winners” and “losers.” Shade-tolerant forbs and trees were negatively impacted outside exclosures, while species associated with higher understory light levels, intermediate/shade-intolerant forbs and exotics, were benefited.
5. *Synthesis and applications.* Forest community response to canopy openings cannot be entirely predicted from current species compositions and/or initial gap areas. Even in forests with relatively low deer densities (6.5 - 9.3 deer km⁻²), white-tailed deer herbivory can influence the trajectory of post-disturbance plant communities. It appears that herbivory may be a mechanism for decreasing β -diversity along environmental gradients, in temperate forests.

Introduction

Plants must overcome a variety of limiting, environmental factors to successfully establish, reproduce, and grow. These external factors can be categorized into two groups, stressors and disturbances (see Grime 1977), and plants have evolved with an array of life history traits to deal with both. Grime (1977) classified plants as competitors, stress-tolerants, or ruderals based on their abilities to cope with different levels of stress and disturbance (low stress/low disturbance, high stress/low disturbance, and low stress/high disturbance, respectively). The term “generalist species,” however, is often used to describe species adapted to a wide range of both (e.g., Krauss et al. 2004; Rooney

et al. 2004, 2007). This high level of flexibility allows generalist species, both native and exotic (Wiegmann and Waller 2006), to expand their populations or invade new sites when native and/or habitat specialist species are in decline (i.e., passenger model; MacDougall and Turkington 2005), a phenomenon that has been linked to habitat degradation (Rooney et al. 2007). Since generalist species are often widely distributed (Wiegmann and Waller 2006), they are able to capitalize on periods of high stress or disturbance at multiple sites, ultimately reducing regional spatial diversity (McKinney and Lockwood 1999). Therefore, generalist species expansion is considered a mechanism of biotic homogenization (McKinney and Lockwood 1999; Olden and Poff 2003): it increases genetic, taxonomic, and/or functional similarity between communities (Olden and Rooney 2006).

In many ecosystems, ungulate herbivores may be promoting the expansion of generalist species. Ungulate herbivory reduces the abundance of palatable, native species, which favors the establishment and survival of unpalatable exotic species (reviewed by Vavra et al. 2007). Herbivory also alters ecosystem processes (e.g., nutrient cycling) that influence environmental conditions for plant growth (Hobbs 1996). Although the impacts of acute herbivory on native plant diversity can be quite severe (e.g., densities ≥ 25 deer km^{-2} ; Augustine and Frelich 1998; Horsley et al. 2003; Webster et al. 2005), changes in biodiversity in systems with low deer densities (e.g., < 8 deer km^{-2} ; deCalesta 1997) are not always apparent and depend on local species abundances (Augustine et al. 1998). For example, Augustine et al. (1998) showed white-tailed deer (*Odocoileus virginiana* Zimmermann) grazing had little influence on the population dynamics of a native forb, *Laportea canadensis* (L.) Weddell, when it was abundant, but when it was scarce growth

and reproduction were severely impacted. Many plant communities have existed with elevated herbivore populations for several years (Rooney 2001; Côté et al. 2004) and may have stabilized under persistent herbivore pressure (i.e., alternate stable states; Stroymayer and Warren 1997). Therefore, some plant communities may be most vulnerable to generalist species invasions immediately following disturbance, a time when species assemblages are inherently in a state of flux (Sousa 1984).

In temperate forest ecosystems, canopy disturbance plays a key role in structuring plant communities (see Frelich 2002). The elevated gap light environment promotes the establishment of new plant species (i.e., gap-phase regeneration; Brokaw 1987) and the release of advance regeneration. Although the influence of overstory removal on plant community composition has been well documented (Runkle 1981, 1982, 1998; Runkle and Yetter 1987; Mladenoff 1990), the impacts of disturbance scale (i.e., canopy gap area) on herbivore-plant interactions are not well understood (Wisdom et al. 2006). The formation of new canopy gaps elevates local levels of mammalian herbivory (as reviewed by Royo and Carson 2006) and ungulates will modify foraging behaviors to adjust to changes in browse patch size (Shipley and Spalinger 1995). Higher light levels also increase foliar nitrogen concentrations (e.g., *Acer* species; Lei and Lechowicz 1998), possibly making large gaps (longer daily duration of direct sunlight; Canham et al. 1990) more attractive than small gaps to herbivores. In addition, Tripler et al. (2002) showed that nitrogen (N) fertilization significantly increased browsing frequency on luxury N consumers (e.g., *Acer saccharum* Marsh.). Individual plants in small gaps, on the other hand, may have higher probabilities of sustaining herbivore damage; white-tailed deer tend to browse a higher percentage of stems and take more bites per stem as patch size

(i.e., number of stems) decreases (Shipley and Spalinger 1995). Consequently, the scale of overstory disturbance (i.e., gap area) may be an important driver of herbivore influence on forest plant communities.

In order to assess how ground-layer plant communities respond to two interacting disturbances, overstory removal and ungulate herbivory, 20 artificial canopy gaps were installed in a hemlock-hardwood forest during the winter of 2002-2003 and 46 deer exclosures were constructed around a randomly selected subset of sample plots in early spring 2005. During the summer of 2007, I measured vegetation response. I hypothesized that (1) herbivory would influence ground-layer community response to gap formation by shifting species compositions (control plot vs. exclosure plot) and (2) these shifts would either (a) be more pronounced in large gaps due to increased browse availability (i.e. large gaps would be more attractive to deer than small gaps) or (b) more distinct in small gaps because of the higher probability of individual plant mortality from ungulate browsing (i.e., small gaps have less browse available).

Materials and Methods

Study area

This artificial canopy gap experiment was conducted in a hemlock-hardwood forest at Michigan Technological University's Ford Forestry Center (46°57'N 88°29'W) near Alberta, Michigan. Alberta is located in the western half of Michigan's Upper Peninsula. The climate of the study area is moderated by Lake Superior, with mean summer and winter temperatures of 17.4°C and -9.8°C, respectively (Berndt 1988). Total mean annual precipitation is 87.4 cm which includes an average winter snowfall

amount of 382.5 cm (Berndt 1988). Soils in the canopy gaps ranged from cobbly silt loams to fine sandy loams (Berndt 1988) and deer densities in the region have been estimated to range from 6.5 deer km⁻² in the spring to 9.3 deer km⁻² in the fall (Mayhew 2003).

Experimental design

Twenty artificial canopy gaps were installed during the winter of 2002-2003 (Table 2-1) by removing clumps of low quality hardwood species from hemlock stands. In total, seven small gaps (50 – 150 m²), seven medium gaps (151 – 250 m²), and six large gaps (251 – 450 m²) were created. Gap areas were calculated as eight-sided polygons. Within each gap, four to twelve (depending on initial gap size), 1 m² plots were installed for vegetation sampling. Random distances and azimuths from gap center (monumented with rebar) were used to position sample plot centers. Up to three plots in each gap were randomly chosen for deer exclosures. These 1 m radius mini-hoop deer exclosures were constructed from 15 cm² heavy gauge wire mesh (height: 1.52 m). This design excludes white-tailed deer but not snowshoe hare (*Lepus americanus* Macfarlani).

Plant community response

During the summer of 2007, I sampled the vegetation plots in the twenty artificial canopy gaps. In each 1 m² sample plot, I estimated the percent cover of vegetation by species (except bryophytes), coarse woody debris by decay class (decay classes 1 – 5; see Sollins 1982), and bare soil. In addition, I measured the slope (%) and aspect (Table 2-1) of each plot and took a digital hemispherical photograph 1.37 m above each plot center to

quantify the understory light environment (Table 2-2). Photographs were analyzed with the software WinSCANOPY (WinScanopy 2005).

To quantify the amount of deer browsing in each gap, I recorded the incidence of browse for all control plot *Acer* saplings (height ≥ 30 cm; Frelich and Lorimer 1985). Percent of individuals browsed was calculated by dividing the number of stems that exhibited deer browse damage in each control plot by the total number of stems present. The proportion of shoots browsed on each individual was also calculated. Only the previous year's growth was examined for browse damage. The number of *Acer* saplings per hectare was calculated by dividing the total number of control plot saplings per gap by the number of control plots and multiplying the quotient by 10,000. All values (percentage of individuals browsed, proportion of shoots browsed, and stems per hectare) were averaged for each gap and then for each gap size class.

Statistical analysis

I used the ordination technique nonmetric multidimensional scaling (NMS; McCune and Mefford 2002) to relate plant species composition patterns in the artificial canopy gaps to the environmental variables measured. All variables (species percent covers and environmental) were averaged by gap and plot type (control or exclosure) for a total of 40 sample units (20 artificial canopy gaps x 2 plot types). Multiple linear mixed effects regression, implemented in the statistical interface R (R Development Core Team 2008), was then used to analyze the effects of significantly (as determined by the NMS ordination) associated environmental variables (fixed effects) on vegetation functional group cover (response variables: shrub, tree, forb, graminoid, cryptogam [non-seed

plants], exotic) with gap as the random effect. I employed mixed effects statistical methods to account for the hierarchical structure in the experimental design (Schabenberger and Pierce 2002). The vegetation sample plots were clustered within artificial canopy gaps, therefore I could not assume that individual sample plots were independent. First, I fit the full model for each functional group and then removed non-significant ($\alpha = 0.05$) fixed effects one at a time until only significant terms remained. Competing models were compared using Akaike's Information Criterion (AIC; Weisberg 2005).

I also used Permutational ANOVA as implemented in the software package PermDisp (Anderson 2004) to test for variability in species composition between the control and exclosure plot groups for all 20 artificial canopy gaps. This technique employs a distanced-based test for homogeneity of multivariate dispersions (Anderson 2004). I used the Sorenson distance measure (Bray-Curtis measure with a presence/absence transformation) to calculate mean distances from group centroid for control and exclosure plot species compositions and to test for a difference in dispersion between these two groups (Anderson et al. 2006).

To further evaluate species composition and abundance in the sample plots, I created species richness and diversity (Shannon Diversity Index) rarefaction curves with the software EcoSim (Gotelli and Entsminger 2001). Rarefaction compensates for differences in sampling intensity between groups (Gotelli and Colwell 2001). First, I evaluated all species, both native and exotic and, second, only native species. Since rarefaction curves for both groups exhibited similar patterns in both species richness and diversity, only results from the former analysis are reported here.

Results

Influence of herbivory on plant species composition

The NMS ordination revealed a clear movement of control plots away from exclosure plots in species space for all 20 gaps (Fig. 2-1), indicating dissimilar species compositions for the two plot types (control and exclosure). The final solution of the nonmetric multidimensional scaling (NMS) ordination was three dimensional with Axis 1 and Axis 3 representing the highest proportions of the variance, 0.339 and 0.299, respectively (Table 2-3). The correlation of environmental variables with axis scores revealed that Axis 1 was significantly associated with all three light variables (diffuse, direct, and total) and sample plot aspect and Axis 3 was significantly associated with diffuse light, gap area (2003 and 2007), and coarse woody debris (Table 2-3). Even in small gaps, where there was less light available for plant growth (Table 2-2), control plot species compositions were similar to those associated with increased levels of light (Fig. 2-1). This was despite the lack of any significant variations in light levels between control and exclosure plots ($n = 139$) within a given gap for all three light variables: diffuse light, direct light, and total light ($t = -0.228$, $df = 118$, $P = 0.820$; $t = -0.717$, $df = 118$, $P = 0.475$; and $t = -0.713$, $df = 118$, $P = 0.477$, respectively). When species were plotted by functional group in sample space versus the environmental gradient for diffuse under-canopy radiation (Fig. 2-2), the resulting figure showed that the presence of intermediate and shade-intolerant forbs, exotic species, and graminoids were associated with increasing levels of diffuse light.

Influence of gap size on herbivory

All twenty gaps exhibited signs of white-tailed deer browsing. Browse intensity in small gaps was somewhat less than that observed in medium and large gaps; however, differences between size classes were not significant ($P = 0.261$; Fig. 2-3). Across all gaps size classes nearly 30% of available *Acer* shoots were browsed and 51% of *Acer* saplings had at least one shoot with evidence of browse.

Interacting disturbances: gap size and herbivory

Species compositions in the three gap size classes became more similar due to white-tailed deer herbivory. A test for homogeneity of multivariate dispersions (PermDisp; Anderson 2004) showed that, in general (all 20 gaps considered), control plot ($n = 93$) species compositions are more similar than those of exclosure plots ($n = 46$; $F = 3.992$, $P = 0.0478$, 999 permutations). Mean distance to group centroid (± 1 SE) was 42.18 ± 0.76 and 44.84 ± 1.11 for control and exclosure plots, respectively. When exotic species (Table 2-5) were excluded from the analysis, an even greater difference in dispersion between control plots and exclosure plots was observed (40.68 ± 0.81 and 43.82 ± 1.20 , respectively; $F = 4.835$, $P = 0.030$, 999 permutations).

Herbivory increased compositional similarity across the three gap size classes by altering patterns of species richness and diversity. In large gaps, species richness was higher in control plots than in exclosure plots, but in medium and small gaps the opposite was observed (Fig. 2-4a). In contrast, control plots were more diverse than exclosure plots in small gaps, but less diverse in medium and large gaps (Fig. 2-4b). Overall, large gap control plots had the highest species richness (Fig. 2-4a), but the lowest species

diversity (Fig. 2-4b). Small gap control plots, on the other hand, had the fewest number of species (Fig. 2-4a), but the highest diversity (Fig. 2-4b). Therefore, deer herbivory appears to be facilitating the introduction of new plants at this site, but skewing species abundance and evenness (in comparison to that of exclosure plots).

Shifts in plant community composition can also be attributed to variations in plant functional group responses to herbivory and gap area. Linear mixed effects models revealed that diffuse light, direct light, and the presence of an exclosure were the best predictors of functional group (shrub, tree, forb, graminoid, cryptogam, and exotic) cover in all 20 artificial canopy gaps, but the influence of each variable differed for the six groups (Table 2-4). Tree and forb cover were the only groups positively correlated with the presence of an exclosure ($P = 0.006$ and $P = 0.020$ [Table 2-4], respectively). Increases in diffuse light levels was positively associated with shrub ($P < 0.001$), graminoids ($P = 0.014$), and exotic species cover ($P = 0.028$; Table 2-4), but forbs and cryptogams cover were negatively associated with higher levels of direct light reaching the gap floor ($P = 0.042$ and $P < 0.001$ [Table 2-4], respectively). Therefore, the post-disturbance environment at this site seems to favor generalist species which are both resistant to browsing and tolerant of a variety of light conditions (i.e., gap areas).

Discussion

Herbivory altered the developmental trajectory of the post-disturbance plant community, at this study site, by facilitating the expansion of habitat generalist species. Control plot species compositions for the 20 artificial canopy gaps were more similar to each other than to that of their corresponding exclosure plots (Fig. 2-1) and these shifts in

species compositions from exclosure plots to control plots were strongly associated with increased light levels (NMS ordination results; Table 2-3). Concurrently, weedy, intermediate/shade-intolerant forbs and exotics were positively associated with elevated light environments (Fig. 2-2). While the coverage of these two functional groups benefited from increases in diffuse and direct under-canopy light levels (Table 2-4), that of shade-tolerant forbs and trees did not, and was negatively impacted outside of exclosures (Table 2-4 and 2-5). As a consequence, the expansion of “winner” (McKinney and Lockwood 1999) functional groups is reducing β -diversity in this temperate forest where it appears that herbivory has the ability to make different size treefall gaps “behave” the same way, compositionally.

While differences in browse intensity did not vary significantly between gap size classes, use of the gaps by deer was high, with > 25% of available shoots in medium and large gaps showing evidence of browse during the previous winter. Browsing was also widespread in these gaps with ~ 51% of *Acer* saplings ≥ 30 cm tall having at least one shoot with evidence of browse. Balgooyen and Waller (1995) showed that their browse index, using just *Acer saccharum*, was highly correlated with local deer densities in northern Wisconsin. Similarly, in Pennsylvania, Horsley et al. (2003) found that *Acer rubrum* stem densities declined significantly with increases in deer densities. Consequently, the similarities I observed in control plot species compositions across the range of gap areas (Fig. 2-1) may be attributable, at least in part, to browse intensity.

The term “biotic homogenization” (McKinney and Lockwood 1999) has been widely used to describe the process by which two or more communities become more similar (decreased β -diversity) over time (as reviewed by Olden and Rooney 2006). Deer

herbivory has been identified as a driver of such changes among temperate forest communities in North America (Rooney et al. 2004; Wiegmann and Waller 2006). This study, however, shows that herbivory may also be a mechanism for decreasing β -diversity along environmental gradients within the same community. Olden and Rooney (2006) recognized that homogenization could transpire within communities if species compositions were shifted by dominant or cosmopolitan species. In general, two mechanisms lead to the process of homogenization: the extinction of resident species and the introduction of new species into new areas (McKinney and Lockwood 1999). A variety of introduction and extinction scenarios have been recognized (see Olden and Poff 2003). Deer browsing facilitates both processes through the extirpation of browse-sensitive species (e.g., *Trillium* spp. [Augustine and Frelich 1998]; *Taxus canadensis* [Beals et al. 1960]; *Tsuga canadensis* [Anderson and Katz 1993]), essentially “freeing up” space for browse-tolerant species to establish and compete (e.g., graminoids and ferns; Horsley et al. 2003; Rooney and Waller 2003; Royo and Carson 2006).

At this study site, it appears that herbivory allowed weedy species and exotics (i.e., generalist species) to establish in small and medium gaps by reducing the overall richness of control plots (Fig. 2-4). The loss of species in two functional groups in particular, shade-tolerant forbs and trees, seems to have allowed for this change. For example, *Clintonia borealis* (Ait.) Raf. and *Acer saccharum* had lower mean percent coverages in control plots than exclosure plots for all three gap size classes, while *Hieracium aurantiacum* L. and *Cirsium palustre* (L.) Scop. L. coverages increased (in the small and medium classes and all three size classes, respectively [Table 2-5]). Dominant species alone may not be responsible for the changes in species diversity that were seen;

rare species losses have also been linked to the introduction of weedy and exotic species (Lyons and Schwartz 2001). Although, browsing increased species richness in large gap control plots, it did not increase overall diversity (Fig. 2-4); as a group, large gaps (251 – 450 m²) had lower species diversity than did small or medium gaps despite the wider spatial variation in light environment (Canham et al. 1990). Homogenization is not always associated with reductions in species richness (Wiegmann and Waller 2006) and species additions outnumber species extinctions in some areas (Hobbs and Mooney 1998). As this experiment shows, at some sites increasing the functional similarity between different species assemblages may be more important to the process of homogenization than changes in species richness (Olden and Rooney 2006).

In conclusion, it appears that herbivory has the ability to reduce spatial diversity across forest landscapes by promoting the functional homogenization (i.e., species compositions shifting towards weedy intermediate/shade-intolerant forbs and exotics; Olden and Rooney 2006) of plant communities across environmental gradients (e.g., different scales of overstory disturbance). The results of this study present a new challenge for forest managers; forest community response to canopy openings cannot be entirely predicted from current species composition and/or initial gap areas. In this experiment, outside of exclosures small gaps “looked like” large gaps compositionally five years post-harvest. Therefore, the influence of coinciding disturbances must also be considered if local and regional diversity are to be maintained. While the traditional approach to studying community level change has been to compare species compositions over time for two or more communities (Olden and Rooney 2006), this study used a controlled experimental system to examine plant community response to a gradient of

disturbance intensity. Controlled experiments, such as the one presented here, may provide a novel approach for future studies on the process of biotic homogenization.

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Table 2-1. Gap attributes by size class (small, medium, and large). Gap areas were calculated as eight-sided polygons.

<i>Small Gaps (50 - 150 m²); n = 7</i>					
	Mean	SE	Minimum	Maximum	Median
2003 Gap Area	114.97	11.92	61.20	148.57	128.47
2007 Gap Area	90.16	12.22	51.82	142.67	75.73
% Change in Area	23.93	5.11	11.06	52.88	21.14
% Slope*	11.27	2.20	5.50	23.50	10.50
Aspect *	245.48	25.55	146.00	319.60	251.67
<i>Medium Gaps (151 - 250 m²); n = 7</i>					
2003 Gap Area	199.32	11.76	163.75	249.43	206.60
2007 Gap Area	170.61	13.70	114.27	207.40	189.19
% Change in Area	20.54	4.69	3.74	40.81	19.13
% Slope	11.35	1.90	7.00	21.25	9.92
Aspect	193.89	26.71	103.25	289.67	190.83
<i>Large Gaps (251 - 450 m²); n = 6</i>					
2003 Gap Area	325.83	27.11	273.23	441.47	302.00
2007 Gap Area	309.12	24.28	241.21	418.96	300.13
% Change in Area	9.41	2.78	0.60	18.65	9.32
% Slope	14.72	1.31	11.50	18.88	13.82
Aspect	232.68	31.65	143.75	323.50	161.75

*Measured at each subplot

Table 2-2. Mean under canopy light levels for the three gap size classes (small, medium, and large).

	Control		Exclosure	
	Mean	SE	Mean	SE
<i>Small Gaps (50 - 150 m²); n = 7</i>				
Direct Under-Canopy Radiation *	10.38	1.01	9.65	1.03
Diffuse Under-Canopy Radiation *	1.76	0.05	1.77	0.06
Total Under-Canopy Radiation *	12.14	1.03	11.42	1.05
<i>Medium Gaps (151 - 250 m²); n = 7</i>				
Direct Under-Canopy Radiation	14.11	0.98	13.61	1.34
Diffuse Under-Canopy Radiation	2.31	0.05	2.29	0.07
Total Under-Canopy Radiation	16.42	1.00	15.90	1.37
<i>Large Gaps (251 - 450 m²); n = 6</i>				
Direct Under-Canopy Radiation	14.36	1.02	13.66	1.92
Diffuse Under-Canopy Radiation	2.45	0.06	2.54	0.10
Total Under-Canopy Radiation	16.81	1.02	16.20	1.94

Note: Hemispherical photography was used to quantify the light environment for each gap subplot. Photographs were taken in 2007 at a height of 1.37 m above plot center and were analyzed with the software WinSCANOPY (2005).

*Photosynthetically active flux density under-canopy average for the growing season (mol m⁻² day⁻¹) (WinSCANOPY, 2005)

Table 2-3. Nonmetric multidimensional scaling (NMS) ordination results. Final solution contains three dimensions and a * indicates significant associations ($\alpha = 0.05$) between environmental variables and axis scores.

<i>Correlation of environmental variables with axes</i>						
Environmental Variable	Axis 1		Axis 2		Axis 3	
	r^a	p	r	p	r	p
Cosine (aspect)	-0.354	0.025*	-0.223	0.168	-0.065	0.691
% Slope	-0.071	0.665	-0.14	0.388	-0.211	0.192
Bare Soil	-0.139	0.393	-0.141	0.384	-0.192	0.236
Bark	0.066	0.688	-0.016	0.924	0.105	0.518
Rock	0.079	0.628	0.219	0.176	-0.126	0.438
Root	-0.132	0.415	-0.146	0.369	-0.141	0.387
Stump	-0.203	0.209	0.082	0.615	0.195	0.228
CWD DC-2 ^b	0.243	0.131	-0.226	0.162	-0.336	0.034*
CWD DC-3	0.076	0.641	-0.167	0.302	-0.341	0.031*
CWD DC-4	0.09	0.579	-0.078	0.634	0.25	0.119
CWD DC-5	0.118	0.469	-0.159	0.328	-0.013	0.938
Diffuse Under-Canopy Radiation ^c	0.519	0.001*	-0.118	0.47	-0.466	0.002*
Direct Under-Canopy Radiation ^c	0.528	<0.001*	-0.31	0.051	-0.129	0.426
Total Under-Canopy Radiation ^c	0.555	<0.001*	-0.306	0.055	-0.173	0.286
2003 Gap Area	0.189	0.243	-0.258	0.108	-0.424	0.006*
2007 Gap Area	0.255	0.113	-0.185	0.254	-0.355	0.024*
<i>Proportion of variance represented by each axis</i>						
R^2	Axis 1		Axis 2		Axis 3	
Increment	0.339		0.227		0.299	
Cumulative	0.339		0.566		0.865	

^a r = Pearson correlation

^bCWD DC = Course woody debris decay class

^cPhotosynthetically active flux density under canopy average for the growing season ($\text{mol m}^{-2} \text{day}^{-1}$) (WinSCANOPY, 2005)

Note: Ordination performed in PC-ORD (version 4.25) using the Sorenson distance measure and a random starting configuration. Forty runs were completed with real data and 114 iterations completed for the final solution. Final stress for the three dimensional solution was 13.45.

Table 2-4. Linear mixed effects models for vegetation functional group cover.

Response Variable (% Cover)	Fixed Effect	Estimate	SE	P value	AIC	Likelihood Ratio		R ²
						value	P	
Shrub	Intercept	-67.85	20.17	0.001	1347.46	29.30	<0.001	0.19
	Area 2007 (m ²)	-0.14	0.06	0.048				
	Diffuse Light*	58.22	11.27	<0.001				
Tree	Intercept	46.27	12.16	<0.001	1243.71	20.09	<0.001	0.14
	Diffuse Light	-13.34	5.35	0.014				
	Exclosure	10.35	3.73	0.006				
Forb	Intercept	17.03	2.40	<0.001	1031.25	22.65	<0.001	0.15
	Direct Light*	-0.30	0.15	0.042				
	Exclosure	3.85	1.63	0.020				
Graminoid	Intercept	-4.48	5.82	0.443	1031.25	15.33	<0.001	0.11
	Diffuse Light	6.41	2.57	0.014				
Cryptogams	Intercept	30.72	3.81	<0.001	1155.81	34.98	<0.001	0.22
	Direct Light	-0.81	0.23	<0.001				
Exotic	Intercept	-6.92	3.80	0.071	959.89	19.04	<0.001	0.13
	Diffuse Light	3.90	1.76	0.028				
	Direct Light	0.29	0.12	0.014				
<i>Forbs by shade tolerance rank</i>								
Tolerant	Intercept	15.85	2.30	<0.001	1014.20	27.24	<0.001	0.18
	Direct Light	-0.30	0.14	0.030				
	Exclosure	3.47	1.52	0.024				
Intermediate & Intolerant	Intercept	-3.07	2.03	0.134	786.40	7.34	0.026	0.05
	Diffuse Light	1.98	0.90	0.029				

Note: Gaps (20 levels) were treated as the random effect. The R² applied to the mixed models is a generalization of the classic R² (Nagelkerke, 2001).

*Diffuse and Direct Under-Canopy Radiation = Photosynthetically active flux density under canopy average for the growing season (mol m⁻² day⁻¹; WinSCANOPY, 2005)

Table 2-5. Mean percent cover vegetation (per m²), by species, for each gap size class (small, medium, and large) and plot type (C = control, E = enclosure).

Species	Authority	Common name	Mean Percent Cover					
			Small Gaps		Medium Gaps		Large Gaps	
			C	E	C	E	C	E
<i>Abies balsamea</i>	(L.) P. Mill.	balsam fir	0.3	0.1	1.5	6.7	0.1	0.1
<i>Acer rubrum</i>	L.	red maple	1.4	2.3	1.4	2.4	0.7	1.6
<i>Acer saccharum</i>	Marsh.	sugar maple	15.4	25.3	9.7	13.8	15.7	24.8
<i>Acer spicatum</i>	Lam.	mountain maple	---	T [†]	---	---	0.1	0.1
<i>Adenocaulon bicolor</i>	Hook.	American trailplant	0.1	0.6	---	---	0.2	---
<i>Agrostis gigantea</i> [°]	Roth	redtop	---	---	T	T	T	T
<i>Agrostis hyemalis</i>	(Walt.) B.S.P.	winter bentgrass	---	0.1	T	---	T	---
<i>Agrostis perennans</i>	(Walt.) Tuckerman	upland bentgrass	0.1	---	---	0.1	0.1	0.1
<i>Amelanchier</i> sp.	Medik.	serviceberry	---	---	T	---	---	---
<i>Anaphalis margaritacea</i>	(L.) Benth.	western pearly everlasting	---	---	---	---	0.1	---
<i>Antennaria</i> sp.	Gaertn.	pussytoes	---	---	T	---	---	---
<i>Anthoxanthum odoratum</i> [°]	L.	sweet vernal grass	---	---	0.1	---	---	---
<i>Aralia nudicaulis</i>	L.	wild sarsaparilla	1.7	---	0.6	0.2	0.9	1.5
<i>Aralia racemosa</i>	L.	American spikenard	0.1	---	---	---	---	1.4
<i>Arisaema triphyllum</i>	(L.) Schott	Jack in the pulpit	---	---	0.2	---	---	---
<i>Athyrium filix-femina</i>	(L.) Roth	common ladyfern	7.7	6.1	1.7	2.4	3.1	3.9
<i>Betula alleghaniensis</i>	Britt.	yellow birch	1.4	0.4	0.4	1.0	1.1	1.6
<i>Brachyelytrum erectum</i>	(Schreb. Ex Spreng.) Beauv.	bearded shorthusk	0.2	0.4	0.6	0.4	0.3	1.1
<i>Carex arctata</i>	Boott ex Hook.	drooping woodland sedge	1.1	1.3	1.0	2.5	1.0	2.6
<i>Carex brunnescens</i>	(Pers.) Poir.	brownish sedge	0.1	0.1	0.2	1.1	0.2	0.2
<i>Carex communis</i>	Bailey	early oak sedge	1.2	3.1	1.7	2.7	0.9	2.1
<i>Carex deweyana</i>	Schwein.	Dewey sedge	0.7	---	---	---	0.3	---
<i>Carex gynandra</i>	Schwein.	nodding sedge	0.6	2.1	2.1	4.5	3.2	1.1
<i>Carex intumescens</i>	Rudge	greater bladder sedge	---	0.6	---	0.3	0.1	---
<i>Carex ormostachya</i>	Wieg.	necklace spike sedge	0.3	0.6	0.6	0.6	1.0	0.3
<i>Carex projecta</i>	Mackenzie	necklace sedge	T	---	T	---	0.5	0.2
<i>Carex scabrata</i>	Schwein.	eastern rough sedge	1.6	1.0	0.2	---	1.1	2.1
<i>Carex stipata</i>	Muhl. ex Willd.	owlfruit sedge	---	---	0.2	---	0.1	---

Species	Authority	Common name	Mean Percent Cover					
			Small Gaps		Medium Gaps		Large Gaps	
			C	E	C	E	C	E
<i>Chrysosplenium americanum</i>	Schwein. Ex Hook.	American golden saxifrage	0.1	T	---	---	---	---
<i>Cinna latifolia</i>	(Trev. ex Goepp.) Griseb.	drooping woodreed	---	0.1	---	---	0.4	0.3
<i>Circaea alpina</i>	L.	small enchanter's nightshade	---	0.1	---	---	T	---
<i>Cirsium arvense</i> [°]	(L.) Scop.	Canada thistle	---	---	---	---	0.1	---
<i>Cirsium palustre</i> [°]	(L.) Scop.	marsh thistle	0.2	---	1.3	0.2	3.6	3.0
<i>Clintonia borealis</i>	(Ait.) Raf.	bluebead	0.9	1.6	1.9	5.4	0.7	0.9
<i>Conyza canadensis</i>	(L.) Cronq.	Canadian horseweed	---	---	---	---	T	---
<i>Coptis trifolia</i>	(L.) Salisb.	threeleaf goldthread	---	---	T	---	---	---
<i>Cornus alternifolia</i>	L. f.	alternatleaf dogwood	0.1	---	---	0.4	---	---
<i>Corylus cornuta</i>	Marsh.	beaked hazelnut	1.1	---	---	---	1.7	---
<i>Diervilla lonicera</i>	P. Mill.	northern bush honeysuckle	T	---	---	---	---	---
<i>Doellingeria umbellata</i>	(P. Mill.) Nees	parasol whitetop	---	---	T	---	---	---
<i>Dryopteris carthusiana</i>	(Vill.) H.P. Fuchs	spinulose woodfern	5.5	9.4	5.1	4.8	6.3	8.3
<i>Epilobium ciliatum</i>	Raf.	fringed willowherb	0.1	0.1	T	0.2	0.1	0.2
<i>Equisetum arvense</i>	L.	field horsetail	0.2	0.2	0.1	0.3	1.4	0.3
<i>Equisetum sylvaticum</i>	L.	woodland horsetail	---	---	0.1	0.1	0.4	0.1
<i>Erigeron philadelphicus</i>	L.	Philadelphia fleabane	T	---	---	---	---	---
<i>Eurybia macrophylla</i>	(L.) Cass.	bigleaf aster	---	---	1.0	0.9	0.1	---
<i>Fraxinus nigra</i>	Marsh.	black ash	T	---	---	---	---	---
<i>Galeopsis tetrahit</i> [°]	L.	brittlestem hempnettle	0.7	0.3	0.1	0.1	0.9	0.3
<i>Galium triflorum</i>	Michx.	fragrant bedstraw	0.3	0.6	0.1	0.2	0.6	0.8
<i>Geum canadense</i>	Jacq.	white avens	---	---	T	---	0.2	---
<i>Geum rivale</i>	L.	purple avens	---	---	---	---	T	---
<i>Glyceria striata</i>	(Lam.) A.S. Hitchc.	fowl mannagrass	---	0.1	---	---	0.2	0.2
<i>Gymnocarpium dryopteris</i>	(L.) Newman	western oakfern	2.1	1.3	0.1	---	2.6	0.4
<i>Hepatica nobilis</i>	Schreber	roundlobe hepatica	---	---	---	0.1	T	0.2
<i>Hieracium aurantiacum</i> [°]	L.	orange hawkweed	1.0	0.1	1.5	0.4	0.5	1.1
<i>Hieracium piloselloides</i> [°]	Vill.	tall hawkweed	---	---	0.1	0.1	0.1	T
<i>Huperzia lucidula</i>	(Michx.) Trevisan	shining clubmoss	---	0.1	---	T	---	0.1
<i>Hypochaeris radicata</i> [°]	L.	hairy catsear	---	---	0.2	---	---	---

Species	Authority	Common name	Mean Percent Cover					
			Small Gaps		Medium Gaps		Large Gaps	
			C	E	C	E	C	E
<i>Impatiens capensis</i>	Meerb.	jewelweed	0.4	0.5	0.5	---	T	0.5
<i>Juncus effuses</i>	L.	common rush	---	0.1	---	---	0.2	0.2
<i>Juncus tenuis</i>	Willd.	poverty rush	---	0.1	---	---	T	---
<i>Lactuca canadensis</i>	L.	Canada lettuce	---	---	---	0.3	---	---
<i>Lapsana communis</i> ^e	L.	common nipplewort	0.2	0.2	0.2	0.4	0.3	0.2
<i>Lonicera canadensis</i>	Bartr. ex Marsh.	American fly honeysuckle	1.2	0.3	0.1	0.5	T	0.4
<i>Luzula acuminata</i>	Raf.	hairy wood rush	---	---	---	0.1	---	---
<i>Lycopodium annotinum</i>	L.	stiff clubmoss	T	0.1	0.1	T	0.1	0.1
<i>Lycopodium dendroideum</i>	Michx.	tree groundpine	T	---	1.3	0.6	0.3	0.3
<i>Lycopodium digitatum</i>	Dill. ex A. Braun	fan clubmoss	2.0	---	---	---	---	---
<i>Maianthemum canadense</i>	Desf.	Canada mayflower	3.0	6.7	4.2	4.5	1.2	3.4
<i>Maianthemum racemosum</i>	(L.) Link	feathery false lily of the valley	---	---	T	---	T	---
<i>Matteuccia struthiopteris</i>	(L.) Todaro	ostrich fern	0.6	---	---	---	---	---
<i>Melica smithii</i>	(Porter ex Gray) Vasey	Smith's melicgrass	0.1	---	---	---	0.1	---
<i>Milium effusum</i>	L.	American milletgrass	0.2	0.2	0.1	---	0.1	---
Moss	NA	moss	8.9	4.6	3.6	3.7	5.4	4.3
<i>Myosotis sylvatica</i> ^e	Ehrh. ex Hoffmann	woodland forget-me-not	0.1	0.2	0.1	---	0.1	0.4
<i>Onoclea sensibilis</i>	L.	sensitive fern	T	---	---	---	0.3	0.3
<i>Oryzopsis asperifolia</i>	Michx.	roughleaf ricegrass	0.2	0.6	1.2	0.1	0.1	0.2
<i>Osmorhiza claytonia</i>	(Michx.) C.B. Clarke	sweet cicely	---	---	T	0.1	T	T
<i>Osmunda claytoniana</i>	L.	interrupted fern	---	---	---	T	T	T
<i>Osmunda</i> sp.	L.	fern	---	---	T	---	---	---
<i>Ostrya virginiana</i>	(P. Mill.) K. Koch	hophornbeam	0.2	---	0.1	---	---	---
<i>Oxalis montana</i>	Raf.	mountain woodsorrel	1.0	1.5	---	0.1	0.8	0.3
<i>Phegopteris connectilis</i>	(Michx.) Watt	long beechfern	2.0	1.9	2.4	0.1	0.1	0.2
<i>Picea glauca</i>	(Moench) Voss	white spruce	T	---	0.1	0.1	---	0.1
<i>Pinus strobus</i>	L.	eastern white pine	---	---	T	---	T	---
<i>Plantago major</i>	L.	common plantain	T	---	---	---	---	---
<i>Poa palustris</i>	L.	fowl bluegrass	0.1	0.2	0.1	0.1	0.3	0.3
<i>Polygonatum pubescens</i>	(Willd.) Pursh	hairy Solomon's seal	0.7	0.2	0.2	0.3	0.3	0.4

Species	Authority	Common name	Mean Percent Cover					
			Small Gaps		Medium Gaps		Large Gaps	
			C	E	C	E	C	E
<i>Polygonum cilinode</i>	Michx.	fringed black bindweed	---	---	---	---	0.4	---
<i>Populus tremuloides</i>	Michx.	trembling aspen	0.1	0.3	---	0.3	0.1	0.2
<i>Prunella vulgaris</i>	L.	common selfheal	---	---	---	---	0.1	---
<i>Prunus pensylvanica</i>	L. f.	pin cherry	---	---	0.1	---	0.1	---
<i>Prunus serotina</i>	Ehrh.	black cherry	---	---	---	---	0.4	---
<i>Pseudognaphalium obtusifolium</i>	(L.) Hilliard & Burt	rabbit-tobacco	---	---	0.2	---	---	---
<i>Pteridium aquilinum</i>	(L.) Kuhn	western brackenfern	---	---	1.4	1.9	---	---
<i>Ranunculus abortivus</i>	L.	littleleaf buttercup	---	T	---	---	0.1	0.1
<i>Ranunculus recurvatus</i>	Poir.	blisterwort	0.1	0.1	0.1	---	0.1	---
<i>Rubus alleghaniensis</i>	Porter	Allegheny blackberry	---	---	1.7	2.1	---	---
<i>Rubus idaeus</i>	L.	American red raspberry	21.1	13.2	28.9	35.6	43.3	35.8
<i>Rumex acetosella</i> ^e	L.	common sheep sorrel	---	T	---	---	---	---
<i>Salix discolor</i>	Muhl.	pussy willow	---	---	T	0.1	0.2	---
<i>Salix</i> sp.	L.	willow	---	---	T	---	---	---
<i>Sambucus racemosa</i>	L.	red elderberry	3.3	3.1	0.3	4.9	4.2	6.0
<i>Sanguinaria canadensis</i>	L.	bloodroot	---	---	---	---	0.2	---
<i>Scirpus atrovirens</i>	Willd.	green bulrush	---	---	---	---	0.1	---
<i>Scirpus cyperinus</i>	(L.) Kunth	woolgrass	0.2	---	0.7	---	0.7	0.4
<i>Solidago canadensis</i>	L.	Canada goldenrod	---	---	---	---	---	0.2
<i>Streptopus lanceolatus</i>	(Ait.) Reveal	twistedstalk	0.4	0.7	0.1	0.7	0.8	1.2
<i>Symphyotrichum lateriflorum</i>	(L.) A.&D. Löve	calico aster	0.1	0.2	0.6	2.5	1.0	0.9
<i>Symphyotrichum</i> sp.	Nees	unknown aster	---	---	T	---	---	---
<i>Taraxacum officinale</i> ^e	G.H. Weber ex Wiggers	common dandelion	0.1	---	0.1	---	0.3	0.1
<i>Thuja occidentalis</i>	L.	northern white cedar	---	---	---	T	---	---
<i>Tilia americana</i>	L.	American basswood	---	0.1	T	---	0.3	T
<i>Trientalis borealis</i>	Raf.	starflower	0.2	0.5	0.9	0.8	0.4	0.3
<i>Trillium grandiflorum</i>	(Michx.) Salisb.	white trillium	---	0.1	---	T	---	---
<i>Tsuga canadensis</i>	(L.) Carr.	eastern hemlock	1.0	0.1	0.3	1.1	0.4	0.6
unknown carex	L.	unknown sedge	T	---	---	---	---	---
unknown composite	NA	unknown composite	---	T	---	---	T	---

Species	Authority	Common name	Mean Percent Cover					
			Small Gaps		Medium Gaps		Large Gaps	
			C	E	C	E	C	E
unknown graminoid	NA	unknown graminoid	---	---	---	0.1	---	T
unknown orchid	NA	unknown orchid	T	---	---	---	---	---
<i>Veronica officinalis</i> ^e	L.	common gypsyweed	0.5	3.7	0.8	3.4	2.2	2.1
<i>Viola blanda</i>	Willd.	sweet white violet	2.0	1.2	0.9	0.9	2.5	1.6
<i>Viola macloskeyi</i>	Lloyd	small white violet	0.3	0.2	0.3	0.2	0.2	0.3
<i>Viola pubescens</i>	Ait.	downy yellow violet	---	---	T	T	T	---
<i>Viola renifolia</i>	Gray	white violet	1.8	2.3	0.3	0.3	2.2	1.7
<i>Waldsteinia fragarioides</i>	(Michx.) Tratt.	Appalachian barren strawberry	---	---	---	---	0.3	T

[†]T = trace amounts, *--- = none present, ^eExotic species

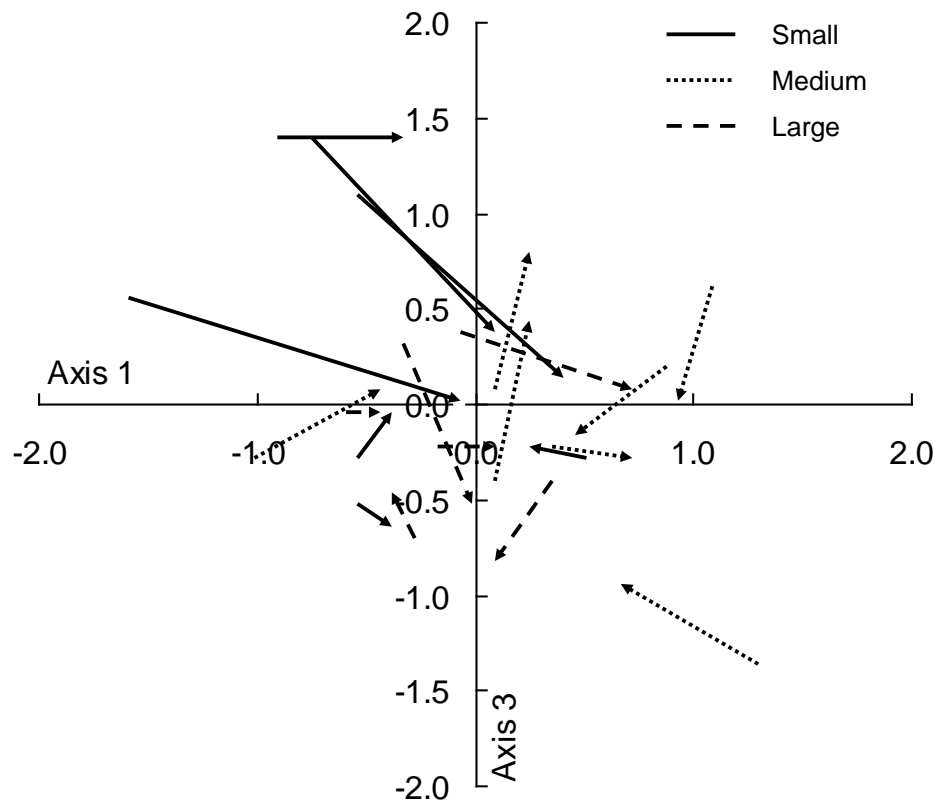


Fig. 2-1 Nonmetric multidimensional scaling (NMS) ordination sample plot scores for axis 1 plotted against axis 3. Vectors represent the magnitude and direction of mean species composition shifts between exclosure (vector origin) and control plots (vector terminal) for each gap ($n = 20$) by gap size class (small, medium, and large).

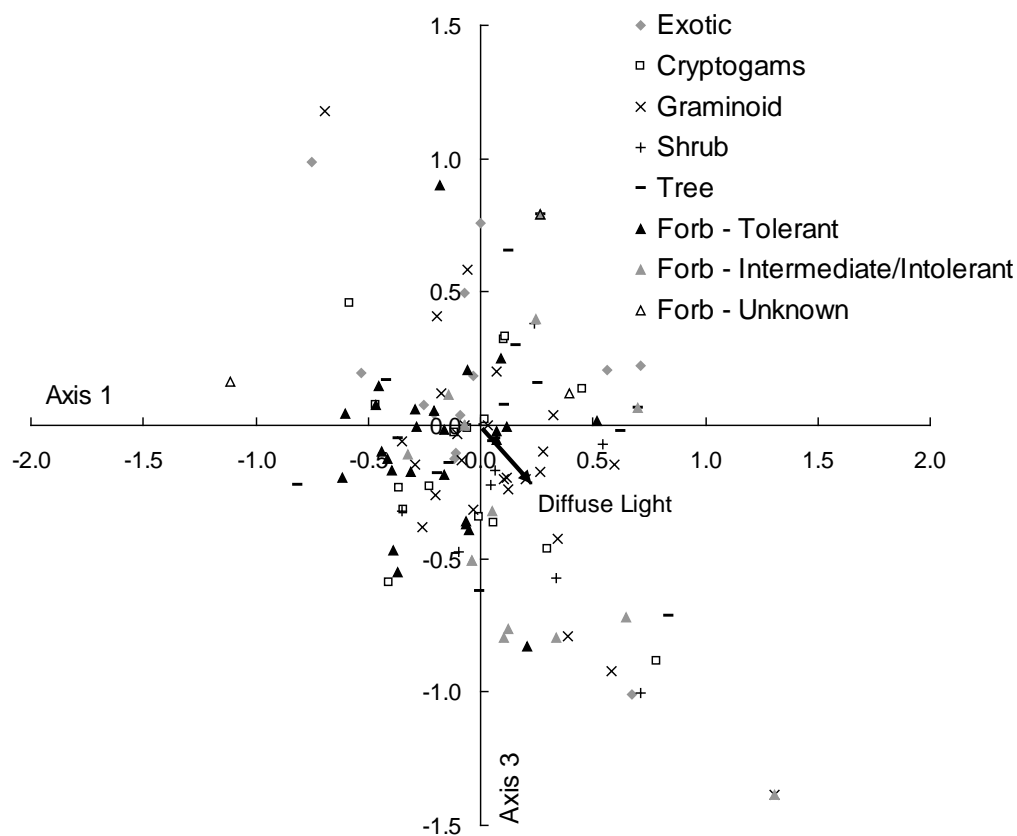


Fig. 2-2 Nonmetric multidimensional scaling (NMS) ordination plot of species functional groups plotted in sample plot space versus the environmental gradient for diffuse light (see Table 2 for values). Species are coded by functional group for ease of interpretation.

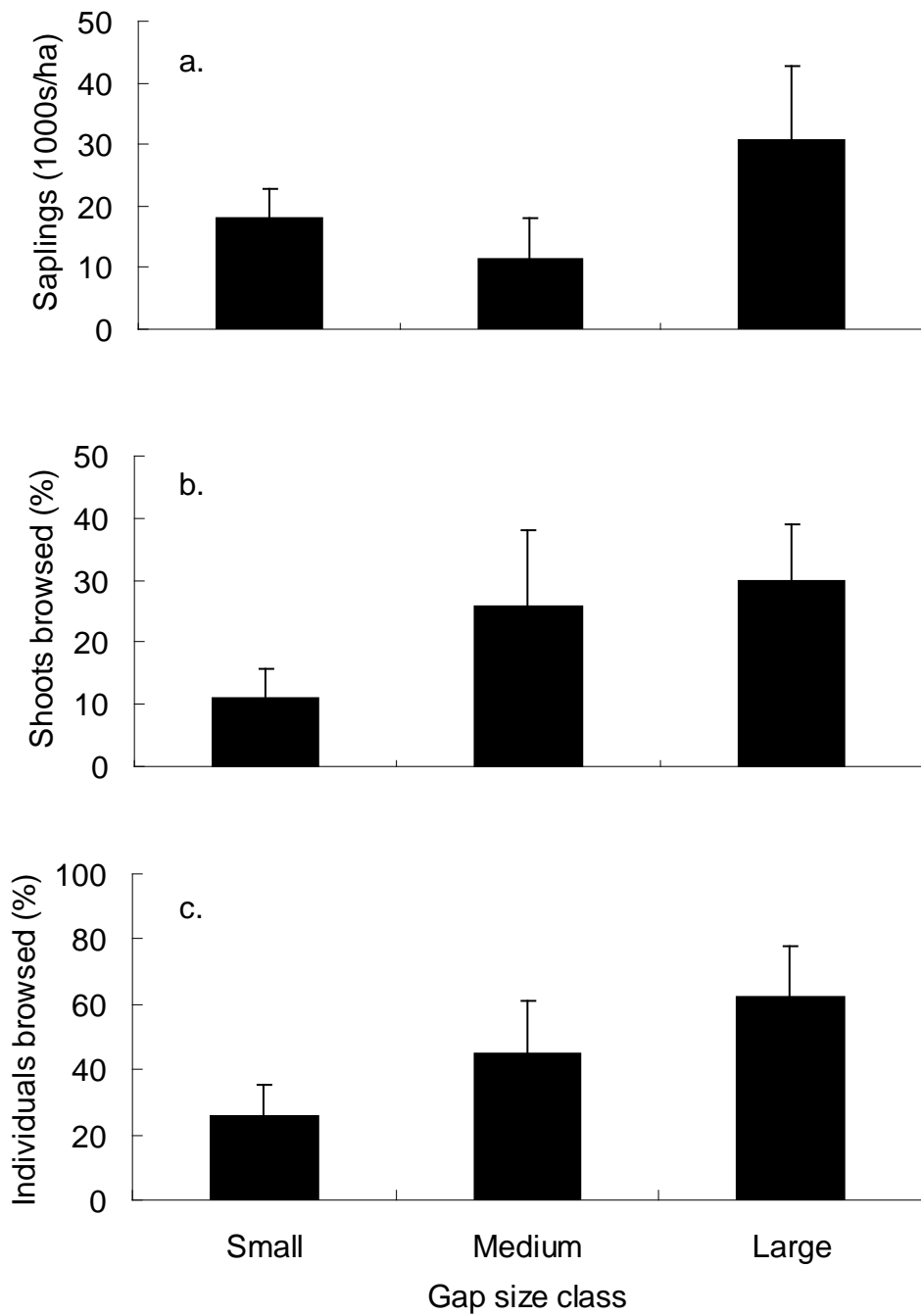


Fig. 2-3 The mean number of saplings (control plot *Acer* species only; height ≥ 30 cm) present (a.), the mean percent of shoots browsed (b.), and the mean number of individuals with at least one shoot browsed (c.) by gap size class (small [50 – 150 m²], medium [151 – 250 m²], and large [251 – 450 m²]).

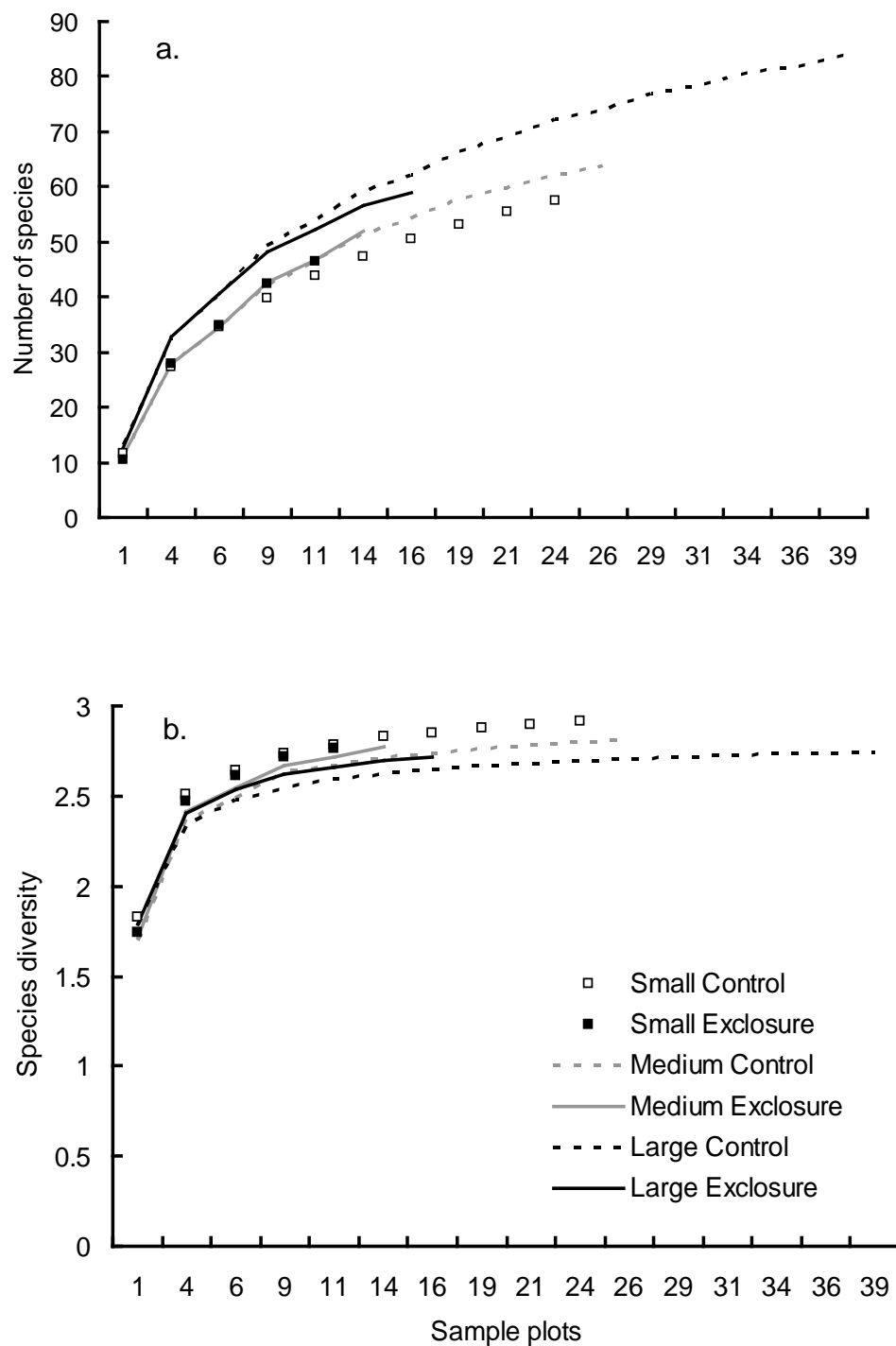


Fig. 2-4 Species richness (a.) and diversity (b.; Shannon Diversity Index) for each gap size class (small [50 – 150 m²], medium [151 – 250 m², and large [251 – 450 m²]) and treatment (control and exclosure) as a function of the number of plots sampled.

CHAPTER THREE

***Acer saccharum* Response to Concurrent Disturbances: The Importance of Stem Layering as an Adaptive Trait**

Abstract

1. For shade-tolerant saplings persisting under heavy forest shade (advance regeneration), the probability of release by disturbance is directly related to longevity. Stem layering has been shown to be an adaptive trait that allows at least one temperate, shade-tolerant species, *Acer saccharum*, to live longer under suppression.

2. I examined the effects of two concurrent disturbances, overstory removal and herbivory, on the regeneration dynamics and release response of *A. saccharum* within 20 artificial canopy gaps ranging in size from 50 – 450 m². Within each opening, up to three 3.14 m² deer exclosures were constructed, and 5 years post-harvest I excavated a random subset of *A. saccharum* saplings for more detailed stem analyses.

3. Five years post-harvest; *A. saccharum* dominated the taller sapling classes across the entire range of gap sizes examined. Evidence of layering was common across all treatments (52%), especially in taller saplings. Neither tissue quality nor browse intensity varied significantly with opening size across the range of conditions examined.

4. The presence of stem layering significantly increased 4-year (excluding year immediately following opening creation) post-disturbance height growth ($P < 0.001$), regardless of gap area or herbivory. The increase in height of layered *A. saccharum* on control plots was in spite of the fact that 70% of these saplings were browsed at least once post-gap creation, compared to 46% of non-layered individuals.

5. *Synthesis*. My results clearly indicate that stem layering is not only an adaptive trait for surviving in suppressed understory seedling banks, but it also plays a potentially important role in the ability of the shade-tolerant species, *Acer saccharum*, to persist under intense herbivory and to respond rapidly to release.

Introduction

Canopy gaps have long been recognized for the critical role they play in the regeneration of many tree species in both temperate and tropical forests (e.g., Watt 1947; Runkle 1981; Brokaw 1987). In order to successfully capture canopy openings, trees utilize a variety of regeneration strategies to ensure that propagules are in place to rapidly capture resources following disturbance. Common strategies include: seed-banking, vegetative reproduction (e.g., stump/root sprouting), and development of a “seedling bank” of advance regeneration (Oliver 1981).

Advance regeneration allows shade-tolerant species to survive as juveniles under suppression by shade in a state of “suspended growth” (Oliver and Larson 1996). This mechanism provides a competitive advantage by enabling shade-tolerant species to wait in the understory for a gap in the canopy to form. Once released from overhead shade, individuals enter a phase of rapid growth in order to capture the gap (recruit into the overstory) before the opening closes as a result of lateral crown expansion by residual overstory trees (Oliver 1981; Canham 1985; Canham 1988; Abrams and Orwig 1996). For many shade-tolerant tree species, release response is not influenced by the number of years spent suppressed (Wright et al. 2000), and in rare cases some species may actually benefit from prolonged suppression (Marshall 1927). Nevertheless, as understory trees

increase in size their tolerance to shade decreases as respiratory demand outpaces photosynthetic capacity (Waring 1987; Givnish 1988; Canham 1989; Pacala et al. 1994). Therefore, in order to successfully reach the canopy and ensure reproductive success, individuals must experience a release event before they grow too large to survive under full shade.

Stem layering (i.e., prostrate stem sections that develop adventitious roots after being buried by leaf litter) may be an important adaptive trait that allows advance regeneration to stay small and grow older while suppressed in the understory (Hibbs and Fisher 1979; Woods 2008). For example, Woods (2008) found that stem layering was a common trait for the temperate, shade-tolerant species *Acer saccharum* Marsh. Approximately 43% of his excavated saplings (n = 943) exhibited layering, and saplings with layering were significantly older than non-layered saplings (Woods 2008). Woods (2008) hypothesized that layered *A. saccharum* saplings would have higher individual probabilities of being released by a disturbance than non-layered saplings, due to increased longevity, and that layered saplings might be more tolerant of stress. Consequently, layering may complement the noted morphological plasticity of *A. saccharum*'s in response to gradients in understory light intensity when small (Beaudet and Messier 1998; Messier and Nikinmaa 2000). Although less prevalent (~3% of individuals), layering also appears to allow the understory tree *Acer pensylvanicum* L to survive longer suppressed (Hibbs and Fischer 1979) and facilitates the formation of multi-stemmed clones (Statler et al. 1997). The formation of adventitious roots on layered portions of stem, however, has more commonly been associated with shade-tolerant conifer species in response to forest floor accretion (e.g., *Picea mariana* (Mill.)

BSP [DesRochers and Gagnon 1997]; *Abies balsamea* (L.) Mill., [Parent et al. 2000]; and *Chamaecyparis pisifera* (Sieb. et Zucc.) Endl. [Hayakawa et al. 2004]) rather than with mechanical oppression of temperate deciduous tree seedlings (i.e., snow loading; Woods 2008).

Another important aspect of longevity in the understory of some forest types is avoiding and/or coping with repeated herbivory (DeLucia et al. 1998). The inability of the shade-tolerant conifer *Tsuga canadensis* (L.) Carr. to tolerate repeated browsing by white-tailed deer (*Odocoileus virginiana* Zimmermann) in shaded understory environments is believed to be a major bottleneck for regeneration of this species (Anderson and Loucks 1979; Frelich and Lorimer 1985; Rooney et al. 2000). *Acer saccharum*, on the other hand, is capable of persisting as a suppressed sapling for decades even with repeated browsing (Stoeckeler et al. 1957; Anderson and Loucks 1979; Frelich and Lorimer 1985), due at least in part to its high biomass allocation to roots (Canham et al. 1996). Advance regeneration faces another potentially important bottleneck immediately following overstory disturbance: over-browsing by herbivores. Tissue quality (e.g., foliar nitrogen) may be high in response to elevated light and resource availability (e.g., *Acer* spp., Lei and Lechowicz 1998) and the pulse of woody and herbaceous growth in new openings makes them attractive foraging sites for many mammalian herbivores (for a recent review, see Royo and Carson 2006). Since light levels (Canham et al. 1990) and foraging behavior are influenced by gap/patch size (Shipley and Spalinger 1995), the size of an opening in which an individual is released may influence its probability of survival and subsequent net height growth.

In order to examine the response of *A. saccharum* to interacting disturbances and the potential role of stem layering, we sampled tree regeneration inside and outside of deer exclosures (exclosure and control plots, respectively) across a range of artificial canopy gap areas (50 – 450 m²) during the summer of 2007. These gaps were established in a hemlock-hardwood forest during the winter of 2002-2003, and deer exclosures were constructed in early spring 2005. In fall 2007, we also excavated a subset of *A. saccharum* saplings (n = 100; from both exclosure and control plots) to determine the influence of browsing and gap light environment on sapling growth rates, tissue quality (C:N ratio), and biomass allocation (root:shoot ratio).

Specifically, I hypothesized that 1) the incidence of herbivory would increase with increasing opening size due to an increase in tissue quality and foraging patch size, 2) resilience to herbivory would increase with increasing opening size since individuals would have a greater capacity for re-growth and a lower individual probability of repeat herbivory, 3) stem layering would provide a competitive advantage and allow *A. saccharum* to tolerate higher levels of stress associated with herbivory by deer.

Materials and Methods

Study area

The forest I studied is located at the Michigan Technological University Ford Forestry Center (46°37'N 88°29'W), which is situated near Alberta, Michigan, in the western portion of the Upper Peninsula of Michigan. Mean summer and winter temperatures for this area are 17.4 C and -9.8° C, respectively, and the mean total annual precipitation is 87.4 cm, which includes 382.5 cm of snowfall (Berndt 1988). The soils

in this study forest are classified as cobbly silt loams and fine sandy loams (Berndt 1988). Small inclusions of mucks occur in depressions. Estimated regional white-tailed deer densities are 6.5 deer km⁻² and 9.3 deer km⁻² for spring and autumn, respectively (Mayhew 2003).

Experimental design

During the winter of 2002-2003, 20 artificial canopy gaps were created in three mixed hemlock-hardwood stands. A range of opening sizes was created by harvesting all merchantable trees rooted within one of four circular plot sizes—50, 150, 250, 350 m². Sub-merchantable trees (> 1 m tall, but < 10 cm diameter at breast height) were felled following the initial harvest and removed from the openings along with coarse logging slash. Crown asymmetry and overlap with the plot edge provided a continuous range of opening sizes. Opening areas (effective gap, Runkle 1982) were calculated as eight-sided polygons and categorized into three size classes: small (50 – 150 m²), medium (151 – 250 m²), and large (251 – 450 m²; Table 3-1). Within each gap, 4 – 12 (depending on gap area), 1 m² permanent plots were established for vegetation monitoring. Plot layout was based on a random distance and azimuth from gap center, which was monumented with rebar. Up to three plots within each gap were randomly selected for installation of a mini-hoop deer enclosure (1 m radius; 1.52 m tall). These enclosures were constructed of heavy gauge wire mesh (15 cm²) which excludes white-tailed deer, but not smaller herbivores such as snowshoe hare (*Lepus americanus* Macfarlane). Gap areas were measured again in 2007 (Table 3-1).

Field methods

Tree regeneration sampling

During the summer of 2007, I quantified the amount of tree regeneration present (fifth post-disturbance growing season) in each of the 20 artificial canopy gaps. In each 1 m² vegetation plot I tallied the number of tree seedlings/saplings present by species and measured the height and diameter of each individual. Seedlings/saplings were placed into one of four height classes (> 0 and ≤ 25 cm, > 25 and ≤ 50 cm, > 50 and ≤ 100 cm, and > 100 cm) for ease of interpretation. For all control plot *Acer* species ≥ 30 cm tall, I also calculated a browse index (Frelich and Lorimer 1985) from the previous year's growth (2006). This value, the proportion of 2006 shoots browsed, was calculated by dividing the number of 2006 shoots exhibiting browse damage by the total number of 2006 shoots present. To quantify the amount of under-canopy light available, I took a digital hemispherical photo above the center of each plot (photo height: 1.37 m). These photographs were analyzed with the software WinSCANOPY (WinScanopy 2005; Table 3-2).

Acer saccharum excavation

In late fall 2007, I excavated the tallest exclosure and control plot *A. saccharum* sapling from each of the 20 artificial canopy gaps. In addition, two more exclosure plot and two more control plot *A. saccharum* saplings were randomly chosen for excavation (stump sprouts and new germinates were excluded from this selection). Because some of the gaps did not contain enough *A. saccharum* saplings in sample plots to complete this sampling matrix, the resultant sample size was 100.

After field excavation, *A. saccharum* saplings were measured in the lab. Total height (cm) from ground level (marked on the stem in the field) to the tip of the terminal bud and diameter (mm) at a height of 10 cm (measured at ground level if sapling height \leq 10 cm) were recorded. Age at ground level was determined from a finely sanded stem cross-section using a dissecting scope. The number of shoots browsed and the total number of shoots present for each year of growth since gap creation were also counted. The proportion of shoots browsed was calculated for 2004 - 2007 growth and averaged. I also measured the total length of annual stem growth increments produced since gap formation and the total length of annual stem growth increments produced three years prior to gap formation. Since *A. saccharum* has a determinate growth form, I excluded the first year of growth post-harvest, which provided four years of post-harvest growth for analysis. Yearly leader growth was identified on each stem using terminal bud-scars. The presence of stem “layering” (i.e., prostrate stem with adventitious roots; see Woods 2008) was also noted for each individual.

After stem measurements were completed, all winter terminal and lateral buds were removed from each seedling and frozen for future nutrient analysis. Stem (aboveground) and root (belowground; includes belowground prostrate stem if present) material was then oven-dried at 90°C until it reached a constant weight. These data were then used to calculate a root to shoot ratio. *Acer saccharum* winter buds were also oven-dried (65°C) for 21 hours and ground with a mortar and pestle. Bud samples were analyzed for carbon and nitrogen content with a Fisons NA 1500 Elemental Analyzer and were calibrated with atropine.

Data analysis

Multiple linear mixed-effects regression, implemented in the statistical interface R (R Development Core Team 2008), was used to examine the effects of gap area, treatment (control or exclosure plot), under-canopy light, browsing, and sapling age (fixed effects) on excavated *Acer saccharum* height growth, root:shoot ratio, and C:N ratio (dependent variables) with gap as the random effect. The effects of layering (presence/absence) and initial sapling height (at the time of gap formation) on height growth were also explored. Since the experimental design contained a hierarchical structure (i.e., vegetation sample plots were clustered within artificial canopy gaps), a mixed effects statistical approach was required (Schabenberger and Pierce 2002). For each response variable, I first fit a full model (i.e., all fixed effects included) and then removed all non-significant ($\alpha = 0.05$) fixed effects, one at a time, until only significant terms remained. Akaike's Information Criterion (AIC; Weisberg 2005) was used to compare competing models and the likelihood ratio was used for comparison against the null model (Crawley 2007). Transformations were used as needed to homogenize error variance and achieve linearity.

Results

Post-disturbance regeneration response

Acer saccharum dominated the post-disturbance regeneration layer. Although, species richness was higher in the ≤ 25 cm height class, *A. saccharum* became increasingly dominant in the larger height classes (Fig. 3-1). This trend was observed

even in the largest gaps. In fact, most of the tallest *A. saccharum* stems (> 50 and ≤ 100 cm and > 100 cm height classes) were located in medium and large gaps (Fig. 3-1).

The percentage of *Acer* sp. shoots (2006 growth) browsed in the gaps by white-tailed deer was quite variable. For saplings ≥ 30 cm in height, the mean browse index (± 1 SE) was highest in large gaps (29.77 ± 9.25), followed by medium (25.91 ± 12.08), and small gaps (10.91 ± 4.95); however, there were no significant differences ($\alpha = 0.05$).

Prevalence and influence of layering in Acer saccharum

Fifty-two percent of the excavated *A. saccharum* saplings ($n = 100$) exhibited stem layering (Table 3-3). For each of the three gap size classes, the proportions of saplings with layering in control and exclosure plots were similar ($G = 7.746$, $df = 5$, $P = 0.171$; Table 3-3). Of the control plot saplings, the proportions of non-layered and layered individuals browsed at least once since gap formation (46% and 70% respectively) were somewhat dissimilar ($G = 2.768$, $df = 1$, $P = 0.096$). The proportions of non-layered and layered individuals, 23% and 39% respectively, that showed signs of repeat browsing (i.e., browsed two or more years since gap formation) were similar ($G = 1.485$, $df = 1$, $P = 0.223$).

The presence of stem layering was a significant predictor ($P < 0.001$) of *A. saccharum* height growth since gap formation. Individuals with stem layering exhibited a greater proportional change in height following gap creation than non-layered individuals in both exclosure and control plots (Fig. 3-2). A categorical variable representing the presence of layering explained 16% of the variation in four-year height growth (LRT = 17.58, $P < 0.001$; Table 3-4). The addition of above-ground sapling age to the model

explained an additional 6% of the variation (Table 3-4). Initial sapling height (at the time of gap formation) was also an indicator of four-year height growth ($P = 0.003$; Table 3-4), with initially taller individuals exhibiting greater post-release growth. The best model (lowest AIC score), however, for predicting absolute height growth included only layering and age (Table 3-4). Sapling age (measured at ground level) was also a significant predictor of root:shoot ratio ($P = 0.002$), but explained only a modest proportion (8%) of the variation in this ratio (Table 3-4).

Influence of light and herbivory on Acer saccharum

Total under-canopy radiation varied significantly between large ($P = 0.025$) and medium gaps ($P = 0.032$) versus small gaps (linear mixed-effects model with gap as the random effect; see Table 3-2 for values). *Acer saccharum* did not show a significant increase in height growth with increasing light ($P > 0.05$). Similarly, winter bud C:N ratio remained relatively constant across the experimental gradient of light intensity for both layered and non-layered individuals in control and exclosure plots (Fig. 3-3a.). Mean proportion of shoots browsed (since gap creation) also showed no clear relationships with an increase in gap area or total under-canopy radiation ($P > 0.05$; Fig. 3-3b.). Linear mixed effects models confirmed these results. Gap area, deer exclusion, and under-canopy light were not significant predictors of C:N or root:shoot ratio ($P > 0.05$). In addition, none of the above variables were significant predictors ($P > 0.05$) of the mean proportion of shoots browsed since gap formation for excavated saplings on control plots. However, the number of years of repeat herbivory since the gaps were created was significantly correlated with the post-release height growth rate of both

layered and non-layered saplings ($P = 0.002$) and root mass ($P < 0.001$, Table 3-5).

There was also evidence that the proportion of shoots browsed was also related to post-release height growth and root mass (Table 3-5). Height growth rate was uncorrelated with winter bud C:N ($P = 0.726$), but was significantly correlated with root mass ($P < 0.001$, Table 3-4).

Discussion

Stem layering was significantly correlated with sapling height growth following release regardless of gap area and herbivory. In fact, height growth in layered *A. saccharum* was greater than that of non-layered individuals despite of the fact that they sustained higher levels of herbivory. These results suggest the well documented ability of *A. saccharum* to persist under high rates of herbivory (e.g., Stoeckeler et al. 1957; Anderson and Loucks 1979; Frelich and Lorimer 1985) may be attributable, at least in part, to the presence of stem layering, which appears to occur with high frequency in northern hardwood forests with heavy snow loads (Woods 2008; this study). Layered portions of stem may allow saplings to acquire additional resources with adventitious roots (Woods 2008) and store extra carbohydrates (Woods 2008; Kobe 1997), two traits that would allow layered saplings to recover more quickly than non-layered saplings from browsing tissue losses (Myers and Kitajima 2007).

Woods (2008) postulated that layered saplings would have higher probabilities of surviving until a release event than non-layered individuals, due to their ability to persist longer as suppressed individuals. Layered saplings have lower leaf area to biomass ratios than non-layered saplings when total stem length (aerial plus layered) is considered

(Woods 2008). Therefore, layered saplings allocate proportionately fewer resources to leaf tissue maintenance than non-layered saplings (Woods 2008). My results suggest that once released, layered seedlings are able to allocate photosynthate more quickly to stem elongation than non-layered seedlings due most likely to lower initial (i.e., at the time of gap formation) respiratory costs. At a given initial height, layered saplings grew faster in height following release than non-layered saplings regardless of within gap variation in local light environment. My results, therefore, suggest that stem layering in *A. saccharum* is an adaptive trait that provides a competitive advantage over non-layered individuals in uneven-aged forests.

Photosynthetic capacity and associated nitrogen levels in the leaves of most *Acer* spp., including *A. saccharum*, are greater in gap than shaded understory environments (Lei and Lechowicz 1998). Many herbivores key in on high tissue nitrogen levels and nitrogen fertilization has been shown to significantly increase browsing frequency on *A. saccharum* (Tripler et al. 2002). Nevertheless, within the range of canopy gap sizes I examined, winter bud C:N ratio showed no consistent pattern with increasing gap area or local light levels. Consequently, counter to my initial hypothesis, increasing gap area did not increase the level of herbivory on *Acer* saplings. This result is consistent with the observation that *A. saccharum* height growth was not influenced by increasing gap area, and earlier research suggesting that *A. saccharum* is released from suppression at much lower light levels than those measured in our smallest gaps (Canham 1988). For example, Webster and Lorimer (2002) found that *A. saccharum* height growth rates leveled off as gap areas approached 100 m², and Ellsworth and Reich (1992) reported that *A. saccharum* can obtain photosynthetic acclimation (mass and area-based photosynthetic

capacity) at ~15% full sunlight (single canopy tree gap [50 m²]). Herbivory, however, was related to growth rate, with fast-growing layered individuals sustaining the greatest level of repeat herbivory. As hypothesized, layered individuals were more resilient to herbivory and achieved greater stature in spite of high levels of browsing. Furthermore, their rapid height growth rate should effectively reduce the time that the terminal leader is susceptible to browse damage, enhancing the likelihood of capturing gaps relative to non-layered conspecifics.

In conclusion, my results suggest that the ability of *A. saccharum* to layer is not only an adaptive trait for surviving in suppressed understory seedling banks (Woods 2008), but also enhances its ability to respond to disturbance. This strategy, which was largely overlooked until recently for temperate deciduous tree species (Woods 2008), may play an important role in the noted ability of *A. saccharum* to persist under repeated herbivory and to respond rapidly to release. Consequently, stem layering is likely an important component of the complex suite of life-history traits allowing shade-tolerant species, such as *A. saccharum*, to dominate a wide variety of post-disturbance plant communities in northern temperate forest (Abrams and Scott 1989; Webb and Scanga 2001; Shields et al. 2007).

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Table 3-1. Mean area (m^2) for the 20 artificial canopy gaps summarized by gap size class (small, medium, and large). Gap area was calculated as an eight-sided polygon.

<i>Small Gaps (50 - 150 m^2); n = 7</i>					
	Mean	SE	Minimum	Maximum	Median
2003 Gap Area	114.97	11.92	61.20	148.57	128.47
2007 Gap Area	90.16	12.22	51.82	142.67	75.73
% Change in Area	-20.78	7.05	-52.88	11.06	-24.11
<i>Medium Gaps (151 - 250 m^2); n = 7</i>					
2003 Gap Area	199.32	11.76	163.75	249.43	206.60
2007 Gap Area	170.61	13.70	114.27	207.40	189.19
% Change in Area	-13.19	7.96	-40.81	14.39	-19.13
<i>Large Gaps (251 - 450 m^2); n = 6</i>					
2003 Gap Area	325.83	27.11	273.23	441.47	302.00
2007 Gap Area	309.12	24.28	241.21	418.96	300.13
% Change in Area	-4.41	4.64	-18.65	14.39	-5.24

Table 3-2. Mean total under-canopy radiation (diffuse plus direct photosynthetically active flux density under-canopy average for the growing season [$\text{mol m}^{-2} \text{day}^{-1}$]; WinScanopy, 2005) for the three gap size classes (small, medium, and large).

Gap Size Class	n	Total Under-Canopy Radiation			
		Control Plot		Exclosure Plot	
		Mean	SE	Mean	SE
Small Gaps (50 - 150 m^2)	7	12.14	1.03	11.42	1.05
Medium Gaps (151 - 250 m^2)	7	16.42	1.00	15.90	1.37
Large Gaps (251 - 450 m^2)	6	16.75	1.02	16.33	1.94

Table 3-3. Number of excavated *Acer saccharum* saplings by gap size class (small, medium, and large) and treatment, the proportion of seedlings with stem layering, and mean height growth since gap formation.

Gap Size Class	Treatment	Excavated Saplings	Proportion with Layering	Mean (\pm 1 SE) four-year height growth (cm)	
				Unlayered Stems	Layered Stems
Small (50 - 150 m ²)	Control	20	0.40	13.2 (2.8)	25.8 (12.1)
	Exclosure	19	0.47	12.5 (1.5)	48.4 (9.6)
Medium (151 - 250 m ²)	Control	12	0.50	18.6 (8.2)	23.5 (6.1)
	Exclosure	16	0.44	26.6 (15.5)	18.6 (5.9)
Large (251 - 450 m ²)	Control	17	0.53	17.6 (6.8)	46.0 (11.9)
	Exclosure	16	0.81	10.6 (1.8)	47.9 (15.5)
Total		100	0.52	16.8 (3.3)	37.5 (5.3)

Table 3-4. Linear mixed-effects models for excavated sugar maple height growth since gap formation (four-year height growth) and root to shoot dry mass ratio (root:shoot).

Model	Response Variable	Fixed Effect	Estimate	SE	P value	AIC	Likelihood Ratio		R ²
							value	P	
I	Sqrt(Four-year height growth)	Intercept	2.73	0.65	0.001	470.53	15.42	<0.001	0.14
		Age*	0.22	0.07	0.001				
II	Sqrt(Four-year height growth)	Intercept	3.96	0.38	<0.001	474.62	14.64	<0.001	0.14
		Initial Height†	0.05	0.05	0.003				
III	Sqrt(Four-year height growth)	Intercept	3.62	0.41	<0.001	464.74	17.58	<0.001	0.16
		Layering‡	1.75	0.49	<0.001				
IV	Sqrt(Four-year height growth)	Intercept	2.36	0.63	<0.001	463.66	24.18	<0.001	0.22
		Age	0.18	0.07	0.029				
		Layering	1.44	0.48	0.025				
V	Sqrt(Four-year height growth)	Intercept	3.30	0.42	0.017	466.99	24.11	<0.001	0.22
		Initial Height	1.50	0.01	0.001				
		Layering	13.99	0.48	0.026				
VI	Root:shoot	Intercept	2.62	0.34	<0.001	353.23	7.35	0.025	0.07
		Age	-0.11	0.04	0.003				
VII	Ln(Four-year height growth + 1)	Intercept	2.37	0.08	<0.001	232.74	77.41	<0.001	0.54
		Ln(Root mass)	0.48	0.04	<0.001				

Note: Gaps (20 levels) were treated as the random effect. The R² applied to the mixed models is a generalization of the classic R² (Nagelkerke 2001)

*Age = age (years) of stem at ground level

†Initial height = height (m) of seedling at time of canopy disturbance

‡Layering = Presence of a “layered” prostrate stem (see Woods 2008), 1 = yes and 0 = no

Table 3-5. Linear mixed-effects models for excavated sugar maple number of years browsed since gap formation (count data; 1, 2, 3, or 4) and mean proportion of shoots browsed versus four-year height growth (cm) and root mass (g).

Model	Response Variable	Fixed Effect	Estimate	SE	P value	AIC	Likelihood Ratio		R ²
							value	P	
I	Years browsed	Intercept	0.52	0.2	0.015	155.55	12.77	0.002	0.23
		4-year height growth	0.02	0.01	0.001				
II	Years browsed	Intercept	0.75	0.14	<0.001	147.14	21.67	<0.001	0.36
		Root mass	0.03	0.01	<0.001				
III	Sqrt(Prop. of shoots browsed)	Intercept	0.18	0.05	<0.001	17.59	4.71	0.095	0.09
		4-year height growth	2.82 x 10 ⁻³	1.30 x 10 ⁻³	0.038				
IV	Sqrt(Prop. of shoots browsed)	Intercept	0.22	0.04	<0.001	18.11	4.13	0.127	0.08
		Root mass	2.58 x 10 ⁻³	1.27 x 10 ⁻³	0.052				

Note: Gaps (20 levels) were treated as the random effect. The R² applied to the mixed models is a generalization of the classic R² (Nagelkerke 2001)

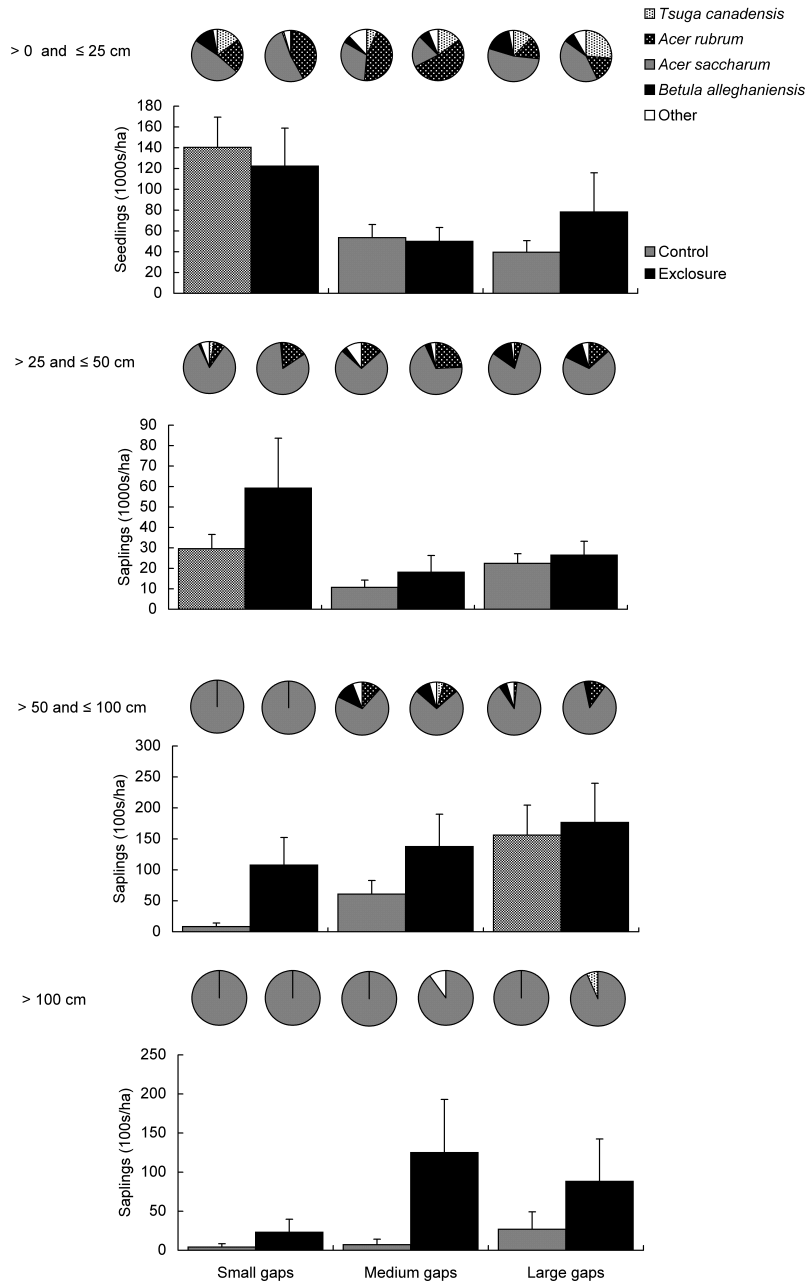


Fig. 3-1. Tree regeneration density (stems ha⁻²) categorized by height, gap size (small, medium, and large), and treatment class (control and exclosure). Pie charts illustrate the proportional representation of individual species within each treatment class combination. Note differences in scale on y-axes.

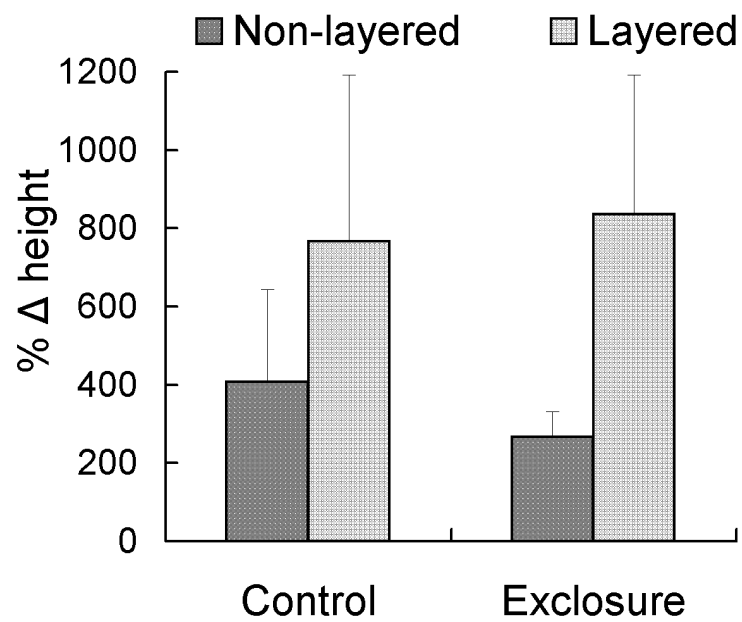


Fig. 3-2. Percent post-release height change after four years by layered (n = 52) and non-layered (n = 48) *Acer saccharum* within exclosure and control plots.

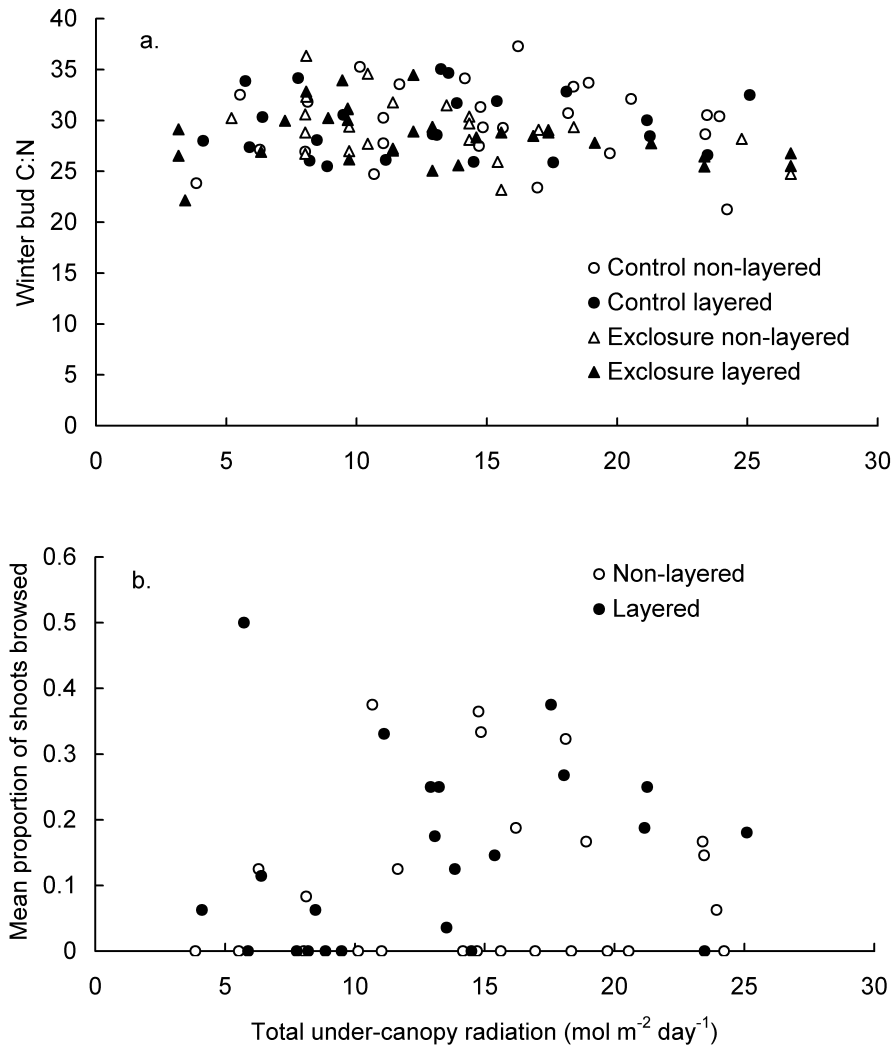


Fig. 3-3. Winter bud C:N (a.) and intensity of browse (control plots only; b.) on layered and non-layered *Acer saccharum* saplings along a gradient of total under-canopy radiation (diffuse plus direct photosynthetically active flux density under-canopy averaged for the growing season [$\text{mol m}^{-2} \text{day}^{-1}$]; WinScanopy 20

CHAPTER 4

Mesic Tree Species Restoration in a Northern Hardwood Forest:

Early Survival and Growth

Abstract

In order to evaluate the effectiveness of underplanting as a restoration tool for *Betula alleghaniensis*, *Pinus strobus*, and *Tsuga canadensis*, I monitored an operational underplanting on private land in Michigan's Keweenaw Peninsula for three years. Three years prior to planting, the study parcel was cut to a residual basal area of 11.5 m²/ha. White-tailed deer (*Odocoileus virginianus*) densities in the region are low due to high winter snowfall amounts. Three years after planting, survival was 59% for *B. alleghaniensis* (n = 302), 57% for *P. strobus* (n = 299), and 60% for *T. canadensis* (n = 302). Factors that influenced seedling 3-year survival and height growth were species specific and appeared to be linked to seedling shade tolerance. Higher levels of direct under-canopy light negatively impacted survival for shade-tolerant *T. canadensis*, but not the midtolerant species *B. alleghaniensis* and *P. strobus*. An increase in diffuse light, however, was linked to higher survival for midtolerant *B. alleghaniensis* and higher 3-year height growth for *T. canadensis*. *Pinus strobus* height growth was significantly associated with an increase in gap fraction (i.e., percent of open sky).

Introduction

In the upper Great Lakes region, forest management practices (past and present) and an overabundance of white-tailed deer (*Odocoileus virginianus* Zimmermann) have reduced the natural regeneration and recruitment potential of three important mesic forest species: *Tsuga canadensis* (L.) Carrière (eastern hemlock), *Betula alleghaniensis* Britton (yellow birch), and *Pinus strobus* L. (eastern white pine). Prior to wide-scale logging (late 1800s and early 1900s) and the frequent slash fires that followed (Whitney 1987), both *T. canadensis* and *P. strobus* were prevalent in the region (as rev. by Abrams 2001). *Tsuga canadensis* now occupies only 0.5% of upland forests (Rooney 2000) and *P. strobus* covers less than 2% of the 4 million acres it once covered (Weyenberg et al. 2004). Although historically comprising a smaller proportion of the northern hardwoods forest type, *B. alleghaniensis* is also underrepresented in second growth stands (i.e., post harvest growth; Godman and Krefting 1960).

In addition to the region-wide elimination of local seed sources, a lack of adequate seedbeds has contributed to reproduction failure for these three species. In *T. canadensis* stands, past logging and slash fires destroyed long-accumulated litter layers that controlled cool and moist forest floor conditions and reduced competition (Mladenoff and Stearns 1993). These disturbances also eliminated large woody debris “nurse logs” that provided warm and moist establishment sites for slow-growing *T. canadensis* and *B. alleghaniensis* (Erdmann 1990; Mladenoff and Stearns 1993). Midtolerant *P. strobus*, on the other hand, is quick-growing and historically relied upon fire to regenerate. Surface fires were a reoccurring disturbance, every 20-40 years, in *P.*

strobis forests and they eliminated competition and prepared mineral seedbeds for regeneration (Weyenburg et al. 2004). *Betula alleghaniensis*, a pioneer species with wind-dispersed seeds, also benefited from fire (Erdmann 1990). Fire suppression, therefore, has altered regeneration dynamics for both *P. strobis* and *B. alleghaniensis*. Fire may also play an important role in the establishment of new *T. canadensis* stands (Maissarow 1941; Cleland et al. 2004).

Even if germination and seedling establishment are successful, herbivory limits overstory recruitment in many areas with high deer densities. *Tsuga canadensis* is a highly preferred winter browse species for white-tailed deer (Beals et al. 1960) and once its terminals are browsed, re-growth potential is greatly reduced (Anderson and Loucks 1979). *Betula alleghaniensis* is also favored browse (Stoeckeler et al. 1957; Beals et al. 1960), especially in the spring and summer months (Rooney and Waller 2003), and will decrease in abundance from light to moderate browsing (Stromayer and Warren 1997). Although preferred to a lesser extent than the other two species, *P. strobis* regeneration is also browsed by white-tailed deer (Smidt and Puettmann 1998).

Restoration of *B. alleghaniensis*, *P. strobis*, and *T. canadensis* is a crucial component of many regional biodiversity conservation efforts. These mesic forest species provide habitat for a wide array of organisms (Holmes and Robinson 1981; Wendel and Smith 1990; Yamasaki et al. 1999), and moderate local environmental conditions (i.e., *T. canadensis*; Ellison et al. 2005). Several silvicultural techniques have been employed to promote the natural regeneration of these species. Methods include even-aged management with shelterwood systems, seed tree cuts, and uneven-aged management

with single-tree and group selection (Lutz and Cline 1956; Lancaster 1985; Smidt and Puettmann 1998; Raymond et al. 2003; Lorenzetti et al. 2008). In addition to promoting natural regeneration for restoration, stands can be underplanted with nursery stock. *Pinus strobus* seedlings have been underplanted in conjunction with various shelterwood and understory treatments throughout the Great Lakes region (e.g., Smidt and Puettmann 1998; Wetzel and Burgess 2001). Less underplanting, however, has been done with planted nursery stock for the other two species, *B. alleghaniensis* and *T. canadensis*.

In order to examine the effectiveness of underplanting for restoring *B. alleghaniensis*, *P. strobus*, and *T. canadensis* to degraded northern hardwood forest communities, I monitored the survival and growth of ~900 seedlings that were operationally underplanted on private land in the Keweenaw Peninsula of Michigan. The objectives of this study were: (1) to identify microsite characteristics that favored or harmed planted seedling establishment and growth and (2) to determine if neighborhood competition influences planting success.

Materials and Methods

Operational underplanting

In 2005, the Michigan Department of Natural Resources (MDNR) operationally under-planted thousands of *Tsuga canadensis*, *Betula alleghaniensis*, and *Pinus strobus* seedlings on a private landowner's parcel (240 acres) located near the tip of the Keweenaw Peninsula of Michigan (47°23'N 87°54'W). The property was harvested three years prior to planting to a residual basal area of 11.5 m²/ha (50 ft²/ac). This site was ideal for planting these three species due to elevated post-harvest, understory light levels.

In addition, white-tailed deer densities are low in the Keweenaw Peninsula due to high winter snowfall amounts (Doepker et al. 1995). Lake Superior moderates the climate of the peninsula, the average winter and summer temperatures are -8.2 °C and 17.4 °F, respectively (Tardy 2006). Mean annual precipitation is 85.6 cm, which includes 555.0 cm of mean annual snowfall (Tardy 2006).

In the spring of 2005, the northern half of the parcel, ~120 acres, was planted with 36,550 3-year old, bare root *P. strobus* nursery stock (McFadden personal communication). Soils in this portion of the property range from moderately well drained, cobbly very fine sandy loams to well-drained, gravelly and cobbly fine sandy loams (Tardy 2006). The following September (2005), 20,580 2-flush (2-year old equivalent) containerized *T. canadensis* and 2,000 2-year old, bare root *B. alleghaniensis* were planted on the remaining 120 acres at the southern end of the parcel (McFadden personal communication). The soils in this portion of the property are similar to those described for the northern half, but include depressions with 0 – 20 cm of muck over very cobbly fine sandy loam.

Seedling monitoring

Shortly after each of the two planting phases (June and September, 2005), ~300 individuals of each species were tagged (*B. alleghaniensis*, *P. strobus*, and *T. canadensis*) to monitor for survival and growth. Seedlings were uniquely identified with numbered metal tags. Each tag was secured to a wire ring that was placed around the base of the seedling. From the northern portion of the parcel, *Pinus strobus* study seedlings were

randomly selected with the requirement of a minimum distance of 5 m between individuals to reduce interdependence. *Tsuga canadensis* and *B. alleghaniensis* seedlings were selected from the southern portion of the parcel with the following constraint that only 2,000 *B. alleghaniensis* were planted; therefore, individuals that met the minimum distance requirement (5 m minimum distance between individuals of the same species) on the planting line were tagged. The nearest *T. canadensis* was also selected. Initial seedling heights and diameters were recorded shortly after planting. Height was measured as the total length of the outstretched stem from ground level to tip of the terminal bud, and diameter was measured at a height of 10 cm above ground level with electronic calipers (measured at ground level if seedling < 10 cm tall).

During the period of late June – early August 2006, microsite conditions, competition from nearest neighbors (woody species only), and light conditions were assessed for each study seedling (Table 4-1). Several microsite characteristics were measured: slope (%), aspect, percent bare soil within a 1 m radius, percent herbaceous plant cover within a 1 m radius, and percent coarse woody debris (CWD) cover within a 1m radius (Table 1). To assess competition, the four nearest woody neighbors (Frelich et al. 1998) were measured for three strata: (1) understory – study seedling vertical height to <2 m tall, (2) midstory – 2m to <10 m tall, and (3) overstory – 10 m and taller. The diameter and height of each competitor was recorded and the distance between each competitor and the study seedling was measured. The light environment at the location of each study seedling was also quantified with a digital, hemispherical photograph. Photographs were taken directly above each seedling at a height of 71 cm and were

analyzed with the software WinSCANOPY (WinScanopy 2005). Light environment was measured as the mean direct and diffuse photosynthetically active flux density for the growing season ($\text{mol m}^{-2} \text{ day}^{-1}$) for *B. alleghaniensis* and *T. canadensis* and as gap fraction (i.e., the fraction of pixels classified as open sky) for *P. strobus* (WinScanopy, 2005). In June of 2007 and 2008, I revisited each seedling to assess survival and in 2008 we measured height and diameter growth.

Statistical analysis

Binary logistic regression models, implemented in the statistical environment R (R Development Core Team 2008), were used to identify factors that best predict *B. alleghaniensis* and *T. canadensis* survival after two growing seasons and *P. strobus* survival after three growing seasons. I also used the statistical environment R to explore seedling height growth over the same study periods with multiple linear regression models. Height growth was calculated by subtracting initial seedling height (at the time of planting) from final seedling height (measured June 2008). For both models (survival and height growth), I first fitted a full model, which included initial seedling dimensions (height and diameter) and environmental variables (see Table 4-1), after which non-significant parameters were removed one at a time until only significant terms remained. Non-significance was further verified by re-addition of the removed variables to the reduced model. Log-likelihood and Hosmer-Lemshow tests were used to assess statistical significance of the binary logistic regression models. The proportion of variability in

height growth explained by each multiple linear regression model was determined by calculating adjusted R^2 (Weisberg, 2005).

After developing our base models (described above), I introduced competition variables to each height and survival model to determine if woody plant competition from the four nearest neighbors in three strata (understory, midstory, and overstory) explained any additional variation. A distance-dependant competition index (adapted from Hegyi 1974) was calculated for each study seedling using the following equation:

$$\sum (D_j / (D_i (Dist_{ij} + 1)))$$

where D_j = diameter of the competitor plant, D_i = diameter of the study seedling, and $Dist_{ij}$ = distance between study seedling and competitor. Competition was summed for each of the three strata, the understory and midstory strata combined, and all three of the strata combined. Competition index variables were included in the final survival and growth models only if they were significant ($\alpha = 0.05$) upon addition to the base models.

Results

Planted seedling survival

Survival for the three study species was similar after three years ($G = 0.61$, d.f. = 2, $P = 0.737$). Fifty-nine percent, 57%, and 60% of *B. alleghaniensis*, *P. strobus*, and *T. canadensis* seedlings, respectively, were alive in June 2008 (Fig. 4-1). For all three species, the highest rates of mortality were observed following the first growing season, but patterns in seedling mortality differed across the three years. In June 2006, *P. strobus* exhibited 40% mortality after experiencing one growing season and one winter, but additional losses were minimal: 2% in 2007 and 1% in 2008 (Fig. 4-1). In contrast,

mortality in June 2006 following only one winter (i.e., seedlings planted in September 2005) was 9% for *B. alleghaniensis* and 15% for *T. canadensis*. After the first growing season and one additional winter, however, mortality increased to 39% for *B. alleghaniensis* and 34% for *T. canadensis* in June 2007. Further losses in 2008 (following two growing seasons) were small, 2%, for *B. alleghaniensis* and slightly higher, 6%, for *T. canadensis*.

The effects of microsite environment and competition (measured 2006) on planted seedling survival also differed for the three study species. An increased probability of *B. alleghaniensis* survival was associated with taller initial seedling heights ($P < 0.001$), higher levels of diffuse under-canopy light ($P < 0.001$), and an increase in understory competition ($P = 0.02$; Table 4-2). The probability of *P. strobus* survival, on the other hand, was only positively associated with an increase in percent cover of bare soil ($P < 0.001$; Table 4-2). Likewise, the probability of *T. canadensis* survival was negatively associated with only one factor, direct under-canopy light ($P = 0.001$; Table 4-2).

Planted seedling height growth

For surviving individuals that exhibited positive height growth over the study period, the factors that influenced height growth differed by species. Larger initial diameters ($P = 0.001$) and higher herbaceous cover ($P = 0.001$) were correlated with increased *B. alleghaniensis* height growth (whole model $F = 12.34$, d.f. = 2, 83, $P < 0.001$; Table 4-3). *Pinus strobus* height growth, on the other hand, was only significantly associated with gap fraction ($F = 13.33$, d.f. = 1, 162, $P < 0.001$; Table 4-3) with higher

growth rates associated with declining canopy cover. Higher levels of under-canopy diffuse light ($P = 0.001$) were correlated with increased *T. canadensis* growth, but an increase in bare soil coverage was associated with decreased height growth ($P = 0.021$; whole model $F = 5.54$, d.f. = 2, 124, $P = 0.005$; Table 4-3).

Discussion

Planted seedling survival

Factors that were significantly correlated with survival for the three study species, *B. alleghaniensis*, *P. strobus*, and *T. canadensis*, can be linked to seedling shade tolerance. In the southern portion of the property, the quality of understory light influenced *B. alleghaniensis* and *T. canadensis* survival differently, despite similar mean levels of direct and diffuse under-canopy light (Table 4-1). Higher levels of diffuse light were correlated with the probability of survival for midtolerant *B. alleghaniensis*, while higher levels of direct light decreased survival for shade-tolerant *T. canadensis*. *Betula alleghaniensis* requires relatively high light levels for successful seedling establishment with 40 – 50% full sunlight optimizing root development (Erdmann 1990). *Tsuga canadensis* seedlings, on the other hand, can persist for decades under deep shade and require stable soil moisture for establishment (Godman and Krefting 1960). Although *B. alleghaniensis* and *T. canadensis* species are closely associated in northern hardwood forests (Godman and Lancaster 1990), differences in seedling shade tolerance allows them to fill different microsite niches when planted under similar growing conditions.

Betula alleghaniensis survival was also positively associated with taller initial seedling heights and higher levels of understory competition. In the southern portion of this study site, an increase in woody, understory competition may indicate an increase in microsite quality (i.e., higher light and/or soil moisture; Burton 1993), as I observed variation in both topography (e.g., slope and aspect; Table 4-1) and soils. *Pinus strobus* survival on the northern half of the property, however, may be linked to reduced competition. Survival for this midtolerant species was only significantly associated with percent bare soil, a characteristic that might be linked to reduced competition and/or higher understory light. Many of these individuals were planted along skidder trails, which lacked overhead canopy cover and exhibited extensive soil scarification. This species requires at least 20% full sunlight for seedling survival (Wendel and Smith 1990) and reduced understory competition benefits natural regeneration (Cornett et al. 1998).

The survival rates (~ 60%) observed for planted seedlings at my study site differ from those found in other studies. For example, Hannah (1990) reported 30% survival after 6 years for rooted *B. alleghaniensis* cuttings in Vermont and <10% survival for an earlier planting of containerized seedlings on the same site. Mortality was attributed to a hot dry period post planting, *Rubus* competition, and browsing by white-tailed deer (Hannah 1990). The survival rates for this *P. strobus* planting, on the other hand, appear low. Noland et al. (2001) reported 77 – 91% five-year survival for both bare root and containerized nursery stock, but growing conditions were more uniform. Although I report short term survival (three year), the reduced rates of mortality following first

growing season losses suggest that survival rates should remain relatively steady in the near future.

Planted seedling height growth

Factors that were correlated with positive height growth for planted seedlings were different than those that predicted survival. For *B. alleghaniensis*, initial diameter and surrounding herbaceous cover were strongly associated with height growth. At this study site, depressions with seasonal inundation supported the most herbaceous plant growth. The soils in these areas have higher accumulations of organic material (Tardy 2006), a characteristic that promotes higher *B. alleghaniensis* growth (Tubbs 1969). Greater heights, however, can also be a sign of reduced seedling vigor. Greater height to diameter ratios in this species have been linked to higher levels of competition and an increase in stem apical death (Lorenzetti et al. 2008). *Tsuga canadensis* height growth was positively associated with higher diffuse light levels and negatively associated with higher percentages of bare soil. Areas of bare soil tended to be on steep slopes and on skidder trails, two areas with the potential for reduced soil moisture and higher levels of direct sunlight. Planted *T. canadensis* seedlings in the Alleghenies showed greatest growth on north facing slopes with partial canopy cover (Godman and Lancaster 1990). *Pinus strobus* height growth, on the northern half of the property, was positively influenced by decreased canopy cover. Other studies also link greater *P. strobus* seedling height and diameter growth to light availability (Smidt and Puettmann 1998; Saunders and Puettmann 1999). For *P. strobus* planted on former agricultural sites and *Pinus*

resinosa Aiton clearcuts in Connecticut, unprotected seedling (i.e., no protection from herbivory) height growth after seven years was significantly associated with initial stem height, root collar diameter, and number of first-order twigs (Ward et al. 2000).

Conclusions

Underplanting appears to be an effective tool for restoring *B. alleghaniensis*, *P. strobus*, and *T. canadensis* to this degraded northern hardwood forest community. Survival rates in this study indicate that, in the absence of high white-tailed deer densities, successful establishment of underplanted seedlings can occur in recently harvested stands. At our study site, which was harvested to a residual basal area of 11.5 m²/ha, understory light levels were variable and were significantly correlated with planted seedling survival and/or growth. My models suggest that planted *T. canadensis* seedling survival might increase with higher residual stand densities, since the amount of direct radiation at a given location depends on how much of the solar track is blocked by overhead vegetation (Ackerly and Bazzaz 1995). Also, the retention of overstory trees with more transparent crowns (e.g., *Quercus rubra* L.) to increase diffuse light transmission would benefit *T. canadensis* growth. Midtolerant *B. alleghaniensis* and *P. strobus* survival was not negatively impacted by canopy openness at this site. This suggests that plantings of these two species would do well at other low-density sites and *B. alleghaniensis* survival may also be enhanced from treatments that further increase diffuse light.

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Table 4-1. Mean (\pm 1 SD) initial dimensions and environmental attributes for planted seedlings by species. Percent bare soil, herbaceous cover, and coarse woody debris (CWD) were measured for a 1 m radius circle surrounding each study seedling.

Species	n	Initial dimensions		Aspect	% Slope	Microsite conditions			Light environment		
		Height (cm)	Diam. (mm)			% Bare Soil	% Herb	% CWD	Gap Fraction*	Diffuse light†	Direct light†
<i>Betula alleghaniensis</i>	302	30.9 (7.3)	2.2 (0.5)	201.8 (58.9)	9.1 (6.2)	12.0 (15.1)	27.9 (26.6)	10.4 (12.7)	----	2.2 (0.5)	15.6 (5.2)
<i>Pinus strobus</i>	299	20.9 (6.1)	3.3 (1.3)	259.4 (78.5)	17.0 (7.6)	12.6 (23.6)	24.7 (25.8)	2.0 (6.0)	23.4 (6.9)	----	----
<i>Tsuga canadensis</i>	302	16.1 (4.1)	1.0 (0.3)	198.2 (54.9)	9.7 (6.2)	14.4 (18.9)	24.2 (24.8)	12.8 (16.4)	----	2.3 (0.5)	15.9 (5.1)

* Gap fraction = fraction of hemispherical photograph pixels classified as sky (WinScanopy, 2005)

† Diffuse and direct light = diffuse and direct below-canopy radiation measured as the photosynthetically active flux density under-canopy average for the growing season ($\text{mol m}^{-2} \text{day}^{-1}$) (WinSCANOPY, 2005).

Table 4-2. Multiple binary logistic regression models of planted seedling survival (live = 1, zero otherwise) after two growing seasons for *Betula alleghaniensis* and *Tsuga canadensis* and after three growing seasons for *Pinus strobus*.

Model					Model fit								
Species	Parameter	Coefficient	SE	P	Odds ratio			Hosmer-Lemeshow			Log-Likelihood		
					Estimate	95% CI		χ^2	df	P	χ^2	df	P
<i>Betula alleghaniensis</i>	Intercept	-4.26	0.87	<0.001				7.80	8	0.454	-187.77	3	<0.001
	Initial height	0.06	0.02	<0.001	1.06	1.03	1.10						
	Diffuse light*	0.95	0.25	<0.001	2.61	1.59	4.26						
	Understory competition	0.14	0.06	0.02	1.15	1.02	1.29						
<i>Pinus strobus</i>	Intercept	-0.01	0.13	0.926				1.86	3	0.603	-195.25	1	<0.001
	% Bare soil	0.03	0.01	<0.001	1.03	1.01	1.04						
<i>Tsuga canadensis</i>	Intercept	1.66	0.41	<0.001				11.18	8	0.192	-198.05	1	0.001
	Direct light*	-0.08	0.02	0.001	0.92	0.88	0.97						

*Diffuse and direct under-canopy radiation = photosynthetically active flux density under-canopy average for the growing season ($\text{mol m}^{-2} \text{day}^{-1}$; WinSCANOPY, 2005).

Table 4-3. Multiple linear regression models of height growth (ΔH = end height – initial height) over two growing seasons for *Betula alleghaniensis* and *Tsuga canadensis* and over three growing seasons for *Pinus strobus*. Only surviving individuals with positive height growth ($\Delta H \geq 0$) were included in these analyses.

Species	Equation*	d.f.	F	P	adj R ²
<i>Betula alleghaniensis</i>	$\Delta H = -1.72 + 3.27(\text{initial diameter}) + 0.07(\text{percent herbs})$	2, 83	12.34	<0.001	0.21
<i>Pinus strobus</i>	$\Delta H = 10.47 + 0.60(\text{gap fraction})$	1, 162	13.33	<0.001	0.07
<i>Tsuga canadensis</i>	$\text{sqrt}\ddagger(\Delta H) = 1.44 + 0.59(\text{diffuse light}\dagger) - 0.001(\text{percent bare soil})$	2, 124	5.54	0.005	0.07

*All variables in the models were significant at $\alpha = 0.05$

† Diffuse under-canopy radiation = photosynthetically active flux density under-canopy average for the growing season ($\text{mol m}^{-2} \text{day}^{-1}$; WinSCANOPY, 2005).

‡ Square root transformation used to normalize the response variable

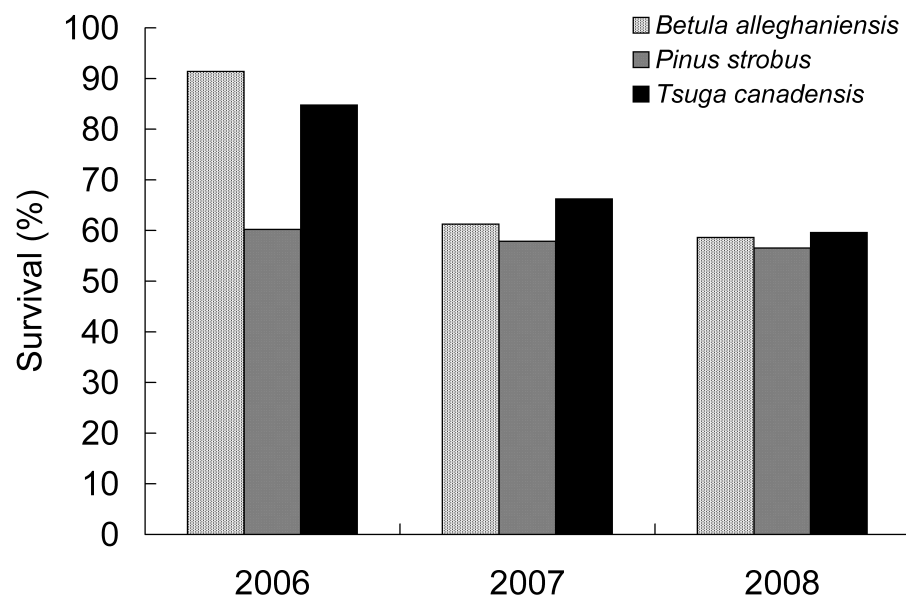


Figure 4-1. Percent survival for planted seedlings by survey year. Survival was tallied late May – early June in 2006, 2007, and 2008. Year 2006 indicates survival after the first growing season for *Pinus strobus* seedlings (planted June 2005) and survival after the first winter for *Betula alleghaniensis* and *Tsuga canadensis* (planted September 2005).

CONCLUSIONS

My goal for this dissertation work was to determine how interacting disturbances influence plant community dynamics in hemlock-hardwood forests. I examined plant community response and planted seedling survival and growth across a range of environmental conditions. The four chapters of this dissertation report important findings from four different studies and discuss their implications for hemlock-hardwood forests. In addition, when these chapters are considered collectively, some important themes emerge regarding plant community dynamics under contemporary disturbance regimes.

Although white-tailed deer densities seem low in some areas of the Upper Great Lakes region (e.g., Baraga county; 6.5 – 9.3 deer km⁻² [Mayhew 2003]), they may still be well in excess of historic levels. For example, deer densities in the western portion of Michigan's Upper Peninsula are twice as high as they were prior to European settlement (Doepker et al. 1995). These discontinuities may explain, in part, why current levels of white-tailed deer herbivory are so detrimental to contemporary forest plant communities (Côté et al. 2004; Rooney 2001; Stromayer and Warren 1997). Chapter 2 shows that herbivory essentially homogenizes forest plant communities following disturbance by facilitating the establishment of generalist species. In addition, Chapter 1 suggests that for highly palatable species, such as Canada yew and eastern hemlock (that are experiencing widespread recruitment failure due to white-tailed deer; Alverson et al. 1988; Beals et al. 1960), recovery may not be possible amid current deer densities. The findings of both of these chapters warrant concern; it appears that selective foraging by white-tailed deer is reducing both functional and taxonomic diversity in forest plant communities. As

reported in chapter 3, sugar maple is much better equipped for dealing with these stresses than the other four mesic tree species that I studied (Canada yew, eastern hemlock, eastern white pine, and yellow birch) and will continue to dominate the landscape given current disturbance regimes.

In the absence of high levels of herbivory (e.g., inside deer exclosures), understory light availability and quality are strongly associated with early survival and growth for Canada yew, eastern hemlock, eastern white pine, and yellow birch. For both Canada yew and eastern hemlock, two extremely shade-tolerant species (Godman and Lancaster 1990; Martell 1974), establishment was negatively correlated with high levels of direct light, but growth was positively correlated with high levels of diffuse light. Midtolerant yellow birch and white pine (Erdmann 1990; Wendel and Smith 1990), in contrast, can tolerate the high post-disturbance light levels following forest harvest, and exhibit higher growth rates in areas with higher levels of diffuse light and canopy openness, respectively. These results suggest that although all four species are associates in the northern hardwoods forest type, each species has its own specific microsite requirements for establishment that need to be considered when planning future regeneration and restoration projects.

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