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Impacts of Harvesting On Regeneration, Productivity, and Floristic Diversity of Quaking Aspen and Northern Hardwood Ecosystems

REPORT TO THE MINNNESOTA FOREST RESOURCES COUNCIL

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No. RR- 0301
March, 2001

Alaina L. Berger
Department of Forest Resources

Principal Investigators
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George Host, Natural Resource Research Institute
John Zasada, USDA Forest Service, North Central Research Station

Project Staff
Alaina Berger, University of Minnesota
Melissa Arikian, University of Minnesota
Bruce Moreira, University of Minnesota

Study site selection was aided through consultation with foresters from the USDA Forest Service- Chippewa N.F. Marcell and Deer River Ranger Districts, Minnesota Department of Natural Resources, University of Minnesota Cloquet Forestry Center, and Minnesota counties- Aitkin, Pine, and St. Louis.

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March 29, 2001

Dear Council members,

I am pleased to submit the final report and updates for several components of the research project: *Impacts of Harvesting on Regeneration, Productivity, and Floristic Diversity of Quaking Aspen and Northern Hardwood Ecosystems* to the Minnesota Forest Resources Council. I have compiled 4 subdocuments into one master document that is numbered consecutively for ease of reference. In general this report should cover the final phase which focused on a retrospective evaluation of harvested areas as well as the second, ongoing phase which monitors a harvesting treatment (case study) in order to help link the findings from the "retrospective" to the "actual" harvesting operation.

More specifically sections of the report cover:

1) Impact of harvesting on soil compaction and aspen regeneration - Master's thesis of Melissa Arikian on pages *i* - 102, (note summaries and conclusions for chapters 2 and 4 are on pages 37 and 86 respectively),

2) Impact of harvesting on soil compaction and floristic composition - manuscript ready to be submitted to the journal Ecological Applications spring of 2001 on pages 103-127, (note Management implications on pg.113),

3) An update on project status for the Boone Sale - a case study on pages 128-136, and

4) Impact of harvesting on sprouting success and growth - a preliminary status report on pages 137-150.

I will be happy to provide additional copies and further information on the various components as planning needs of the council arise.

Sincerely,

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Soil disturbance and residual forest canopy influence tree regeneration in aspen and northern hardwood stands of Minnesota

A THESIS
SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL
OF THE UNIVERSITY OF MINNESOTA
BY

Melissa Jean Arikian

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
MASTER OF SCIENCE

March 16, 2001

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Funding for this study was provided by the Minnesota Forest Resources Council, USDA Forest Service North Central Research Station, and the University of Minnesota College of Natural Resources. I would like to thank my committee members D. Grigal and J. Zasada, and especially my advisor K. Puettmann for their integral assistance with my work. I would also like to thank A. Berger for her never ending support with this project, a number of foresters for their assistance in study site selection, and R. Kirk and M. Counte for reviewing earlier drafts of the thesis.

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Thesis Introduction

This master's thesis is divided into four chapters. All study sites investigated for this thesis were chosen with the same criteria outlined in the methods sections, and pre-investigation all underwent the same treatments (soil disturbance and overstory removal along a gradient of harvest regimes). Although similar in many respects, due to contrasts in their ecology and response to harvesting between aspen dominated and northern hardwood stands, I chose to break this paper into four components: Chapters one and two investigate aspen regeneration, and chapters three and four investigate northern hardwood regeneration.

Chapter one consists of a literature review that summarizes information from a wide variety of publications concerned with aspen regeneration after timber harvest, and the influences and interactions of soil compaction and residual overstory basal area. This review introduces and summarizes results from previously conducted research, while chapter two elaborates on the study I conducted. Chapter two is written in journal submission format for Forest Science and reports the findings concerning aspen regeneration along a gradient of harvest regimes. In this chapter I present specific information about differential aspen density and height response gradients and interactions of soil compaction and residual basal area.

Chapter three consists of a literature review summarizing literature concerned with northern hardwood regeneration after harvest, the influences of soil compaction and residual overstory basal area on vegetation, and how responses vary depending on shade tolerance of tree species. This review introduces and summarizes information from previous data, while chapter four elaborates on research from the project presented in chapter two. Chapter four parallels the findings in chapter two regarding the effects of harvest activity on soil compaction. In addition it expands upon the influence and interactions of that soil compaction with residual overstory basal area on northern hardwood regeneration and advance regeneration according to tree species' shade tolerances. Results from this study help to better understand the ecology and current management considerations of aspen and northern hardwoods in northern Minnesota.

Chapter 1

Soil compaction and residual forest canopy influences on tree regeneration in aspen dominated stands: A literature review

Background

Natural disturbance regimes interrupt the natural progression of stand development and may cycle the forest to early successional stages. Northern forest ecosystems undergo perpetual cycles of perturbation. Historically, the Great Lakes forests, specifically of Minnesota, contained vast expanses of white pine (*Pinus strobus* L.), red pine (*P. resinosa* Aiton.), jack pine (*P. banksiana* Lambert.), and northern hardwood species including aspen (*Populus spp.)* (Curtis 1959, Ahlgren and Ahlgren 1983). Before the 20th century the timber industry began to change ecosystem dynamics at a drastic rate, most notably with its removal of white and red pines. Many forests in the Great Lakes region now covered with aspen (*Populus tremuloides* Michx.) were first harvested starting around 1830 by burning and logging of mature pine and northern hardwood stands (Gates 1930, Kilburn 1957, Curtis 1959), and have been periodically harvested since then. Prior to significant logging disturbance, aspen stands comprised a smaller component of the Great Lakes forest (Ahlgren and Ahlgren 1983). Due to its regeneration strategies, aspen was able to rapidly invade recently burned, blowndown, or logged areas. Trembling aspen has the widest natural distribution of any tree in North America (Perala 1990). The aspen forest dominated by trembling (*P. tremuloides* Michx.) and bigtooth aspen (*P. grandidentata* Michx.) comprises over one-third of Minnesota's timberland, representing 5.1 million acres in 1990 (Miles et al. 1995).

Management objectives regarding the harvest and utilization of aspen have changed over the past 100 years. Aspen was treated as an aggressive, weedy species that prevented other, more desirable tree species from regenerating on a site. Developments in wood technology and utilization created a new demand for aspen as a valuable commodity. Currently, forest managers consider aspen to be an economically profitable species, and have formulated management plans to perpetuate this valuable resource (Raile and Hahn 1982). As a result of its availability and high demand, harvesting of aspen has increased in the Lake States. Many early reports of aspen ecology focused on maintaining adequate environmental conditions to maximize regeneration efforts (Weigle and Frothingham 1911, Zon 1928, Zehngraff 1949, Stoeckeler and Macon 1956, Graham

et al. 1963). Although aspen species take advantage of and regenerate in recently disturbed areas, a wide variety of factors influence the eventual success or failure of an aspen stand. These factors include but are not limited to stand, soil, and harvesting conditions. This paper focuses on several important variables affecting aspen regeneration, including soil disturbance, season of harvest, and amount of residual overstory.

Timber Harvesting Effects on Soil Disturbance

Harvesting traffic often decreases soil aeration, creates rutting, and damages roots, therefore decreasing the growth potential of roots and aspen's ability to sucker. Rutting occurs when wheels from harvesting equipment break through the soil surface or root mat, creating soil displacement and frequently results in physical injury to extant root systems. Soil compaction often accompanies rutting, both which have significant impacts on the soil's environment. Minnesota's Generic Environmental Impact Statement (GEIS) of 1992 identified soil compaction as a major issue forest managers must focus on in order to maintain forest productivity in Minnesota (Jaakko Pöyry Consulting 1994).

Traffic by logging machinery in a harvested site creates a gradient of disturbance, which can be quantified in part by measuring soil compaction. Pritchett and Fisher (1987) define soil compaction as the reduction in macropore volume with an increase in the volume proportion of solids, caused by some external force. The degree of compaction depends on the type(s) of equipment used and the harvesting intensity applied. The magnitude of soil compaction also depends on soil properties including soil water content, soil particle size distribution, organic matter content, and soil strength (Chancellor 1977, Marshall and Holmes 1979, Grey and Jacobs 1987). Soil strength measures soil particles' resistance to movement and relates the amount of compaction and rutting accrued from harvest machinery traffic.

Many soil properties affect the magnitude of soil compaction resulting from a harvest operation. Soil moisture content is directly related to the magnitude of soil compaction, as wet soils compact more readily than drier soils (Steinbrenner and Gessel 1955, Hatchell et al. 1970, Moehring and Rawls 1970, Wert and Thomas 1981). Soil particle size distribution, or soil texture, also affects the degree of compaction. Although soil texture classes are highly variable, clays are likely to compact to higher bulk densities (Moolman 1981, Grey and Jacobs 1987). Conversely, compaction in soils largely composed of coarse-textured, poorly sorted sands, or non-swelling clays is not influenced strongly by moisture content (Bodman and Constantin 1965, Grey and Jacobs 1987).

Bulk density of a soil is a measure of soil compaction. Bulk density reflects the dry weight per volume of soil in Mg/m^3. Soil bulk density and porosity most directly measure soil compaction in a quantitative manner, and studies frequently use them to express changes due to vehicular traffic (Reisinger et al. 1988). Bulk density increases with the applied force from harvesting machinery, negatively correlates to soil porosity, and in forest soils ranges from 0.2 Mg/m^3 (soils with a high organic matter content) to 1.9 Mg/m^3 (coarse sandy soils). Intermediate ranges for clay dominated soils average around 1.3 Mg/m^3. Resistance to penetration also measures soil compaction in terms of soil strength. Soil compaction due to logging traffic may reduce the soil pore space, significantly affecting seedling root penetration, thus negatively influencing suckering and seedling growth (Hatchell et al. 1970, Martin 1988). Soil cone penetrometers measure the resistance of a soil to penetration, which many researchers correlate to the forces a plant root must push through in the soil medium.

Soil compaction appears most severe on landings, truck roads, and skid trails where machinery traffic is concentrated (Kochenderfer 1977, Case and Donnelly 1979, Martin 1988). Studies found skid trails to have significantly lower aeration porosity and greater bulk density values than of undisturbed portions of the same harvested site (Kabzems 1996). The severity of site damage increases in a non-linear fashion with the number of times heavy machinery drives over an area (Murphy 1982). Most of the

resulting soil compaction/increase in bulk density occurs during the first passes of harvesting equipment (Hatchell et al. 1970, Shetron et al. 1988, Koger et al. 1984, Reisinger et al. 1988, Williamson and Neilsen 2000). Froehlich et al. (1980) showed that 60 percent of the soil compaction on skid trails occurred after only six trips. Skid trail systems are often designed with the intention of minimizing the aerial extent of site disturbance. Moist soils of medium-texture sustain considerable compaction after only the first vehicle trip, so confining harvest machinery to fewer trails minimizes site disturbance. Dry soils of coarse texture are less susceptible to extreme compaction after several trips, so skid trail layout on such soils could cover a greater area than on wet clay soils (Hatchell et al. 1970).

Soil Disturbance Effects on Plant Growth

As soil disturbance occurs, plants experience reduced or halted growth rates due to insufficient soil aeration conditions. The effect of soil disturbance on root penetration in trafficked areas, i.e. skid trails, can have negative impacts on subsequent tree growth (Bates et al. 1990, Navratil 1991, Zasada and Tappeiner 1969, Schier et al. 1985, Corns 1988, Shepperd 1993). This reduction in growth, however, varies with tree species, pre-harvest soil conditions, stand density, and severity of disturbance from harvest machinery (Murphy 1982). Few studies have found no detrimental effects of harvesting equipment on soil conditions (King and Haines 1979), and only few have found actual growth increases along skid trails (Pfister 1969, Stransky 1981). Lack of reduction or increased growth rates on disturbed areas most likely relate to soil amelioration of skid road areas. Most studies report specific quantification of reduced growth resulting from soil disturbance (Bates et al. 1990, Navratil 1991, Schier et al. 1985, Shepperd 1993, Zasada and Tappeiner 1969). Froehlich (1976) found Douglas fir trees exhibiting growth losses of 14% height growth in moderately impacted areas, and of 30% in heavily impacted areas (11-40 % and >40% respectively of their root zone affected by a 10% or greater increase in soil density, respectively). Loblolly pine height growth was reduced by 39 percent in compacted skid road areas as compared to adjacent untrafficked areas (Lockaby and Vidrine 1984). Alban et al. (1994) found aspen sucker density reduced in

compacted areas with average maximum sucker height at 218 cm compared to 282 cm in untreated areas.

Because aspen regenerates through root suckering, regeneration responses reflect its vulnerability to site and soil disturbance. Aspen root sprouts and suckers originate from a shallow root network from the parent stand, and therefore remain vulnerable to site and soil disturbance. In addition to soil compaction, physical injury to root systems comprise the major impact of soil disturbance on aspen's ability to sucker. Root damage can occur with no apparent soil disturbance, significantly decreasing aspen's suckering capacity through fine root injury and death (Shepperd 1993). Rutting and root damage have been shown to significantly reduce sucker density (Shepperd 1993) and height growth (Smidt 1996).

Season of Harvest Effects on Aspen Regeneration

Another consideration influencing regeneration is the season of year at which aspen stands are harvested. Since stored root carbohydrates supply energy for sucker development (Tew 1970), seasonal differences in root carbohydrate content significantly affect sucker vigor (Bates et al. 1990, Ek and Brodie 1975). Root carbohydrate content is highest in early fall, remains at high levels throughout the dormant season, and is lowest in spring due to leaf flush (Schier and Zasada 1973, Tew 1970). Many studies in the Great Lake States conclude aspen suckering occurs at a higher density and with greater height growth when harvest operations take place in the winter months (Weigle and Frothingham 1911, Zehngraff 1946, Stoeckeler 1947, Zehngraff 1947, Stoeckeler and Macon 1956). Aspen stands cut in winter months were found to contain from two to five times the density of aspen suckers as compared to similar stands cut in the summer of that same year (Zehngraff 1946). However, studies conducted in Saskatchewan have found summer harvests to stimulate aspen regeneration, where suckering densities following winter clearcutting were nearly half the quantity as compared to summer clearcutting (Bella 1986, Bella and DeFranceschi 1972). These findings most likely relate to soil warming that occurred in Saskatchewan's extreme northern climate. A recent survey

indicates that 54% of harvesting operations in Minnesota occurred during winter months (Puettmann and Ek 1999).

Another factor responsible for seasonal differences in aspen suckering is the soil conditions. If the soil is frozen, winter logging also results in less site disturbance because soil compaction is minimized (Mace et al. 1971). Also, aspen suckers regenerating after winter harvests are established the following summer, allowing an equal or advanced start with competitive brush vegetation (Zehngraff 1947). Spring and summer harvests may result in aspen suckers being produced in midsummer. These sprouts may die in the following winter due to intense competition from previously established vegetation, improper hardening off (Zehngraff 1946), or damage during harvest.

Residual Overstory Effects on Aspen Regeneration

Aspen is a very shade intolerant species and achieves maximum stocking and growth under open conditions (Schier 1976, Schier et al. 1985, Bates et al. 1989, Perala 1990, Peterson and Peterson 1996). Aspen is a clonal species that requires soil temperatures of at least 20° C (Steneker 1974) to stimulate maximum suckering and development. Traditionally, forest managers have clearcut aspen stands, taking advantage of the manner in which it reproduces rapidly from root suckers following logging or fire (Weigle and Frothingham 1911, Stoeckeler and Macon 1956, Farmer 1962, Schier and Smith 1979, Steneker 1974, Bella 1986). However, recent trends in forest management include leaving reserve trees in clear-cut areas (Puettmann and Ek 1999). Studies have shown that residual overstory left after an aspen harvest produces high levels of shade that can reduce soil temperatures and significantly reduce aspen suckering ability (Zon 1928, Zehngraff 1947, Stoeckeler and Macon 1956, Schier and Smith 1979, Hove and Blinn 1990, Ffolliott and Gottfried 1991).

Current guidelines recommend a conservative level of 2.3 m^2/ha of residual basal area when managing aspen stands for optimal regeneration (Perala 1977, DeByle and

Winokur 1985, Navratil 1991). After four growing seasons Stoeckeler and Macon (1956) found stands with a residual overstory of 4.4 m^2/ha basal area to contain only 150 trees/ha of aspen sprouts, compared to roughly 1,100 trees/ha growing in stands with 0.6 m^2/ha residual basal area. Percent canopy cover also estimates the degree by which a residual canopy shades regenerating aspen stands. To represent degree of shading on aspen regeneration, Huffmann et al. (1999) found increasing residual canopy cover to significantly reduce aspen regeneration. Stoeckeler and Macon (1956) found average annual height growth of aspen sprouts in the lower residual overstory (0.6 m^2/ha) stand averaged to be over three times greater than sprouts growing in the denser overstory (4.4 m^2/ha) stand. Interspecific overstory competition also shades aspen suckers and significantly influences aspen regeneration.

White spruce and aspen residual basal area proved to significantly reduce aspen suckering density (Waldron 1963, Navratil 1991). Areas with residual basal areas of 25+ m^2/ha contained 20% stocking of aspen suckers, compared to over 70% stocking in areas of 5 m^2/ha or less residual overstory. Quaking aspen diameter growth also decreased over 50% from increased competitive conditions of overtopping by other aspen regeneration (Puettmann and Reich 1995). Measured as percent open sky (POS), increased competitive conditions were defined as decreasing POS from 100 to 20%. This type of competitive pressure also significantly decreased aspen height growth and crown volume growth. As a shade intolerant species, aspen also suffers reduced regeneration success from competition with shrub species (Zehngraff 1947). Dense areas of shrubby brush, especially *Corylus cornuta* L. (beaked hazel) resulted in a decrease of about 75 percent in aspen sprouts as compared with shrub free areas (Stoeckeler and Macon 1956).

Productivity of Aspen Stands

Sustaining aspen productivity following a harvest regime largely depends on the quality and density of regeneration (Navratil 1996). Many studies have attempted to model aspen productivity over time based on current growing conditions. Average volumes for 50-year-old aspen stands range from 200 to 400 m^3/ha (Peterson and

Peterson 1992). Foresters commonly use site index to measure site quality. Defined as the average height of dominant and codominant trees in an even-aged stand at a given age (often 50 years), site index is well correlated with a given stand's productive potential (Carmean et al. 1989). Average 50-year site index values for aspen stands in Minnesota range between 50 and 90 (English units), or 15 to 27 (metric equivalents) (Laidly 1979, Carmean et al. 1989). Current research suggests that using site index ignores the need to account for population density influences on height growth (MacFarlane et al. 2000). It is a well-established fact that aspen growth conforms to self-thinning density laws. Early development of sucker-origin aspen stands has been well documented to show rapid sucker growth and rapid natural thinning (e. g. Pollard 1971, Bella and DeFranceschi 1980, Peterson and Peterson 1992). The rate at which this self-thinning density law is applied to individual stands depends in part on local growing conditions, often associated with a site's potential for production, measured by site index (Perala et al. 1995). Therefore there has been an increased need to incorporate additional ecological factors and existing site conditions which will affect the future stand's productivity (Peterson and Peterson 1992).

Introduction to My Study

The abundance of aspen ecology literature lends itself to understanding concepts in optimizing regeneration as a management goal. Many variables influence the success or failure of an aspen management, including the amount of residual overstory remaining, the timing and severity of a harvesting regime, and the resulting soil disturbance. This first chapter focused on quantifiable differences in aspen regeneration resulting from the individual factors listed above. However, current studies have yet to consider the interacting effects of these variables. Chapter two provides solid evidence of the significant impacts these interactions have on aspen regeneration, and the implications they hold for the future composition and productivity of Minnesota's forests.

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Chapter 2

Soil compaction and residual forest canopy influence tree regeneration in aspen dominated stands

Abstract

Impacts of clearcutting and partial harvest on aspen stands were examined at 25 sites in northern Minnesota. In each stand, residual overstory, soil compaction, and tree regeneration were determined along a disturbance gradient in the summers of 1997 and 1998, 4 to 11 years after harvest. I characterized soil disturbance as soil compaction using an Eijkelkamp soil cone penetrometer. Compaction levels on skid trails were higher on sites harvested in the summer than sites harvested in winter. After adjusting for differences in soil compaction, stands harvested in winter were associated with higher relative regeneration stem densities and height growth than on sites harvested in the summer. Relative tree regeneration stem densities and height growth decreased with increasing soil compaction and increasing residual basal area. Predictions of future stand volume at age 50 revealed moderate decreases in productivity resulting from harvest conditions investigated in this study.

Additional Key Words:

tree regeneration, aspen regeneration, *Populus tremuloides*, soil compaction, residual overstory, harvesting effects, aspen productivity

Introduction

Historically, the Great Lakes forests, specifically of Minnesota, contained vast expanses of white pine (*Pinus strobus* L.), red pine (*P. resinosa* Aiton.), jack pine (*P. banksiana* Lambert.), and northern hardwood species including aspen (*Populus spp.)* (Curtis 1959, Ahlgren and Ahlgren 1983). Due to its regeneration strategies, aspen (*Populus tremuloides* Michx.) rapidly invaded stands previously dominated by pine that were burned, blown down, logged, or abandoned after agricultural clearing. The aspen forest dominated by trembling (*P. tremuloides* Michx.) and bigtooth aspen (*P. grandidentata* Michx.) now comprises over one-third of Minnesota's timberland, representing 5.1 million acres in 1990 (Miles et al. 1995). Although aspen species take advantage of and regenerate in recently disturbed areas, a wide variety of factors influence the success or failure of aspen regeneration. These factors include, but are not limited to site, soil, and post harvesting conditions.

Management objectives regarding the harvest and utilization of aspen have changed over the past 100 years; aspen was treated as an aggressive, weedy species that prevented other, more desirable tree species from regenerating on a site. But as a result of its large capacities for natural regeneration and increased importance in the wood products industry, harvesting of aspen has increased in the Lake States. Aspen is a very shade intolerant species and achieves maximum stocking and growth under open conditions (Schier 1976, Schier et al. 1985, Bates et al. 1989, Perala 1990, Peterson and Peterson 1996). Traditionally, forest managers have clearcut aspen stands, taking advantage of the manner in which it reproduces rapidly from root suckers following logging or fire (Weigle and Frothingham 1911, Stoeckeler and Macon 1956, Farmer 1962, Schier and Smith 1979, Steneker 1974, Bella 1986). However, recent trends in forest management include leaving reserve trees in clear-cut areas (Puettmann and Ek 1999). Studies have shown that residual overstory left after an aspen harvest can produce too much shade and significantly reduce aspen regeneration (Zon 1928, Zehngraff 1947, Stoeckeler and Macon 1956, Schier and Smith 1979, Hove and Blinn 1990, Ffolliott and Gottfried 1991). Current aspen management guidelines recommend a maximum of 2.3

m^2/ha of residual overstory basal area when managing aspen stands for optimal regeneration (Perala 1977, DeByle and Winokur 1985, Navratil 1991).

Many studies in the Great Lake States also concluded that aspen suckering occurs at lower densities and with lower height growth when harvest operations take place during summer months (Weigle and Frothingham 1911, Zehngraff 1946, Stoeckeler 1947, Zehngraff 1947, Stoeckeler and Macon 1956, Smidt 1996). Aspen root carbohydrate stores are lowest in the spring and early summer, providing a lesser amount of potential sprouting vigor following summer clearcuts as compared to winter clearcuts (Schier 1981, Schier and Zasada 1973). In addition, if the soil is frozen in winter, logging results in less site disturbance because soil compaction is minimized (Mace et al. 1971) and less physical disturbance to the organic layers.

Because aspen regenerates through root suckering, regeneration success can be closely related to soil disturbance. Harvesting traffic often decreases soil aeration and/or damages roots (e.g. Hatchell et al. 1970, Shetron et al. 1988), therefore decreasing the growth potential of roots and the ability of aspen to sucker (e.g. Youngberg 1959, Hatchell et al. 1970, Stone and Elioff 1998). Logging machinery traffic creates a network of skid roads in harvested sites, and disturbances can be quantified in part by measuring soil compaction. Soil compaction appears most severe in landings, truck roads, and skid trails where machinery traffic is most concentrated (Kochenderfer 1977, Case and Donnelly 1979, Martin 1988, Williamson and Neilsen 2000). The degree of compaction depends on the type(s) of equipment used, machine operator attitude and skill, and harvesting intensity. Soil compaction may reduce the soil pore space; increasing soil strength (Grey and Jacobs 1987), inhibiting tree root penetration, thus negatively influencing growth (Hatchell et al. 1970, Martin 1988).

Tree regeneration responses to harvesting effects can be quantified by measuring the productivity of resulting vegetation. Most studies that have investigated impacts of soil compaction on tree regeneration have not considered residual overstory effects (e. g. Froehlich 1979, Bates et al. 1990, Navratil 1991, Schier et al. 1985, and Shepperd 1993).

Other studies looking at residual overstory effects on aspen regeneration have not incorporated effects of soil compaction (e. g. Huffmann et al. 1999, Stoeckeler and Macon 1956, Perala 1977, and DeByle and Winokur 1985). These previously mentioned studies investigated young aspen stands and have not extended current growth values to rotation age yield predictions. Investigations of modeling site productivity over time on regenerating aspen stands have not incorporated the potentially negative influences of soil compaction or residual basal area on future stand volume (e. g. Ek and Brodie 1975, Raile and Hahn 1982).

This study set out to investigate the interaction of the various factors influencing aspen regeneration following harvest. The first set of hypotheses tested that soil compaction levels on skid trails are greater than areas away from skid trails (Hypothesis 1a), and that summer harvests have higher associated soil compaction than winter harvests (Hypothesis 1b). The second set of hypotheses tested that soil compaction significantly decreases tree regeneration density and maximum height of suckers (Hypothesis 2a), and that this relationship significantly differs between sites harvested in winter versus summer (Hypothesis 2b). The third set of hypothesis incorporates the effects of residual overstory into the relationships established in hypotheses 1a and 2a, and states that there is a significant interaction between increased soil compaction and residual overstory basal that decreases aspen regeneration density and maximum height (Hypothesis 3).

Methods

Study Area and Site Selection

This study included 25 aspen dominated stands in six counties of northeastern Minnesota (Figure 1). Trembling aspen (*Populus tremuloides* Michx.) and bigtooth aspen (*Populus grandidentata* Michx.) comprise the major species indicated by the aspen designation. These stands were clearcut or partially harvested between 1988 and 1994 and measured in the summers of 1997 and 1998, four to eleven (average of six) growing

seasons after harvest. Sites were selected to assure a range of harvest treatment conditions, and fairly homogeneous within site characteristics. The study sites covered four harvest regimes; including summer and winter aspen clearcuts, aspen clearcuts with low hardwood residual basal area (<3 m^2/ha), and aspen cuts with heavy hardwood residual basal area (12 m^2/ha) (Table 1). Study sites were only selected if no recent major disturbances or management activity had occurred since the harvest. Sites investigated in this study had an average quaking aspen site index of 22 m (Table 1).

Study sites were fairly level and had an average slope of 8 percent. The overall mean annual temperature for the study region ranges from 3.8 to 5.6° C, and the overall mean annual precipitation ranges from 66 to 76 cm (Anderson et al. 1996). The study sites exist mainly on till parent materials (Anderson et al. 1996). Soil textural data collected from all field sites indicated that all study sites are located on similar classes of sandy loams and silt loams

All sites were considered aspen harvests, i.e. aspen was the main species cut, with the major residual overstory species being northern hardwoods. Other than aspen, sugar and red maple (*Acer saccharum* Marsh. and *Acer rubrum* L.), basswood (*Tilia americana* L.), northern red oak (*Quercus rubra* L.), and paper birch (*Betula papyrifera* Marsh.) were the most common of the 22 tree species in the residual stand, and composed 82 % of the residual overstory basal area. Trembling and bigtooth aspen were the most common species regenerating, comprising 97 % of the regenerating stems on all aspen sites. Paper birch and red maple were the most common of the 11 non-aspen tree species regenerating, and together composed 2 % of the total regeneration density.

Field Collection and Description of Data

I obtained timber sale maps from the United States Forest Service, Minnesota Department of Natural Resources and several counties in northern Minnesota, from which I chose target locations for subsequent field observations. On each study site, twenty regeneration plots were systematically placed along gradients of disturbance

(Figure 2). Four transects extended from landings or skid trails, into the adjacent areas. Rectangular (2 m x 5 m) plots were established along these transects. The initial plot was placed on a skid trail or opening with subsequent plots established parallel to and at increasing distances from the plot 1. Five plots were established per transect, 0, 2, 2, and 4 meters apart, (i.e., for analysis purposes, the centers of each regeneration plot were respectively 0, 1, 5, 9, and 15 meters from the edge of the skid trail). This approach was followed as closely as possible given specific site conditions. Season of harvest was labeled as winter or summer, but I could not determine whether soil was frozen during the harvest operation. Implications of these methods are described in this chapter's discussion section.

Forest Vegetation

On each regeneration plot, diameters (mm) at breast height (DBH) were measured for all trees > 2.54 cm DBH with a caliper or diameter tape. The origin of all trees within the regeneration plot was noted as sucker, sprout, seed, or residual overstory. Heights (m) were taken for six regeneration stems per species in each regeneration plot using a height pole or clinometer. For each species, trees were grouped into diameter classes and heights were taken for the maximum, intermediate, and minimum DBH per species. Maximum tree height represented the trees that most likely will make up the future composition of the regenerating stand. Residuals were defined as trees left standing after harvest with a minimum DBH of 18 cm. Residual overstory basal area was measured from the center of each regeneration plot using a 1-meter factor prism.

For all aspen clearcut study sites investigated during the 1998 field season (11 out of 13 total), additional tree measurements were taken in smaller subplots. These additional data were intended to better characterize smaller size classes of regeneration trees in aspen clearcuts. Within each regeneration plot, these subsets of data were collected in two 1m x 1m subplots randomly placed in two of the four plot corners. Within each 1 square meter subplot, DBH (mm) and heights (m) were taken for all trees greater than 1 meter in height regardless of DBH using a caliper or diameter tape.

While aspen was the dominant species regenerating on all sites (representing 86 % or greater of stem density) and was the tree species with maximum height on 99 % of the plots, all tree species were included in the analysis. Excluding stems other than aspen would possibly misrepresent the response of tree regeneration to soil compaction and overstory residual basal area.

Forest Soil

As an indicator of soil compaction, the penetration resistance (kPa) of the soil matrix using an Eijkelkamp soil cone penetrometer (Bennie and Burger 1988) was measured in each regeneration plot up to a 15 cm soil depth (ASAE 1990). Force exerted on the penetrometer equaled a uniform rate of approximately 30 mm/sec or slower, and readings were taken when the cone reached 15 cm soil depth. A 1 cm^2 base area cone was used on all but 3 study sites. Penetrometer measurements for the three study sites on which a 2 cm^2 base area cone was used were then converted by the following equation:

$$\text{Cone resistance} = \frac{\text{gauge reading}}{\text{base area of cone (cm}^2\text{)}}$$

A minimum of ten randomly selected penetrometer samples per plot was taken and recorded. All measurements on a given study site were taken within the same day, to ensure that soil moisture conditions were relatively uniform for an entire site. Readings were ignored when it was obvious that the penetrometer hit a rock or a log and those readings were not recorded. Since the mean and median penetrometer values for each regeneration plot were correlated by an r^2 value of 0.99, I used the median value to minimize effects of outlying values.

Ten samples for soil texture analysis were collected from five randomly located points within each study site. For each point, one sample was taken from the 0-25 cm profile, and one sample was taken from the 26-50 cm profile. Texture analysis was conducted in the lab in fall 1998/winter 1999 using a modified hydrometer method (Grigal 1973). Four study sites were chosen on which to investigate the relationships

between soil bulk density, soil water content, and resistance to penetration. Soil sample volume was obtained using the irregular-hole method (Howard and Singer 1981). Each sample was then placed in a paper bag and dried for 48 hours in an oven at 105°. Wet and dry weights were taken with a Mettler PM 34 Delta Range electronic digital balance scale. Soil bulk density and soil moisture data were obtained from these weight differences.

To quantify effects of harvest regimes on tree regeneration, I considered several factors contributing to between-site variability including stand age, site index, study site location, and soil properties. My analysis did not set out to compare the sites directly, instead I assumed within site homogeneity and compared within site trends. I standardized the data for each transect with 100% as the baseline. The plot farthest away from the skid trail (plot 5) was considered a "control" in terms of harvesting impact on soils. Therefore soil compaction, density, and height measurements in all other plots were divided by the respective values found in plot 5, thus calculations "relative density," "relative total density," "relative maximum height," and "relative compaction" or "predicted relative compaction." The methodology applied to this standardization technique assumed that plots farthest from the skid trail (plot 5) always represented the control condition and thus contained the highest density, highest maximum height, and lowest soil compaction when adjusting for overstory density. Apparently, this was not always the case, thus leading to an inflated model intercept and slope. These inflated intercepts may have partially resulted from improper selection of a control condition, harvest treatment, and/or random chance. Residual overstory basal areas reflected absolute values.

Aspen Productivity

To obtain estimates of future aspen productivity on aspen clearcuts, the average 50 year quaking aspen site index value for sites in Table 1 (22 m) was used. For aspen sites with residual basal area, examples were used with 6 m^2/ha of residual basal area, and a site index of 22 m. For the prediction we assumed that the impact of soil

compaction and residual overstory is constant over time. I.e., the relative height difference (expressed as %) between areas on skid trails or landings versus adjacent areas at time of measurement will be the same as height differences at rotation age of 50 years. These differences were interpreted as differences in 50-year site index and volume predictions were derived from normal yield tables for quaking aspen (Perala 1977).

Data Analysis

I conducted all statistical analyses using JMP 3.1.6.2 (SAS Institute Inc. 1996). Unless otherwise noted, relationships were considered significant if $p \leq 0.05$. Simple and multiple regression analyses were used to determine the nature of relationships between soil properties, overstory conditions, harvesting conditions, plot location, and tree regeneration.

To avoid potential interacting effects of residual overstory, only aspen clearcuts were used to analyze soil compaction trends and the effect of predicted compaction on tree regeneration density and height. Aspen clearcut analyses included the smaller subplots to estimate aspen regeneration density (designated as "total regeneration") and height response to soil compaction.

To quantify the levels of soil compaction on and off the skid trail (Hypothesis 1a) I fit linear models predicting relative compaction levels as a function of distance from skid trail. For analysis purposes, I added a standard value of 0.1 to distances from skid trail and conducted a natural log transformation to reflect the nonlinear relationship. Analysis of covariance was used to determine whether this relationship varied between sites that were harvested in winter versus summer (Hypothesis 1b). The full model contained indicator variables for season of harvest on the intercept and slope parameters; while reduced models only included indicator variables on either the slope, the intercept, or neither.

To test whether regeneration density and height were influenced by soil compaction levels (Hypothesis 2a), I fit linear regression models predicting relative total density and relative maximum height as a function of predicted relative compaction (as determined in Hypotheses 1a and 1b). I used analysis of covariance to determine whether this relationship differed between sites harvested in winter versus summer (Hypothesis 2b) as described for Hypotheses 1a and 1b. One transect that was already "flagged" in the field due to its unique location on a side slope, was determined to be an outlier and omitted from the analyses. For relative maximum height analysis, plots were omitted from analysis if there were no trees present. Therefore, total density regeneration analyses contained 80 observations of summer aspen clearcuts and 135 observations of winter aspen clearcuts. Maximum regeneration height analyses contained 104 observations of summer aspen clearcuts and 92 observations of winter aspen clearcuts.

I investigated the effects of residual overstory and soil compaction and their interactions on tree regeneration (Hypothesis 3) using two approaches. First, I fit linear regression models predicting relative density and relative maximum height as a function of predicted relative compaction, residual basal area, and predicted relative compaction times residual basal area and testing the parameters for significance ($p>0.10$). I used analysis of covariance to determine whether these relationships differed between sites harvested in summer versus winter as described for Hypotheses 1a and 1b. Three transects; i.e. 15 plots were omitted from relative density analysis because there were no trees in plot 5. Therefore the relative density analysis contained 483 observations. Plots were omitted from relative height analysis if there were no trees present. Therefore the relative maximum height analysis contained 322 observations.

For the second approach investigating effects of residual overstory and soil compaction on tree regeneration, I fit regression models predicting absolute regeneration density and absolute maximum height as a function of predicted relative soil compaction for each site. Then, the intercept and slope coefficients of each site were regressed against the respective residual basal area. A significant slope of both the intercept and

slope models is an indicator that the effects of soil compaction and residual basal area on regeneration are interactive.

Results

Influence of Timing on Compaction Levels in Aspen Clearcuts

On aspen clearcut sites, median penetrometer values varied across sites (Table 2), individual readings ranged from 300 to 8,500 kPa, and plots farthest from the skid trail represented a range of compaction from 300 to 7,700 kPa (Table 1). Penetrometer readings on plots in the skid trail ranged from 750 to 8,500 kPa. Relative soil compaction decreased significantly with distance (DIST) from the skid trail (Figure 3). Harvesting impacts on relative soil compaction differed between seasons of harvest. Sites harvested in the summer months showed significantly steeper soil compaction gradients (equation 1) than areas harvested in winter (equation 2). I used these results to obtain predicted relative soil compaction (PRED COMP) equations to use for subsequent aspen clearcut analyses:

(summer) [1] PRED COMP = 162.75 kPa - 21.41 kPa [ln (DIST (m) + 0.1)]

(winter) [2] PRED COMP = 116.33 kPa - 5.76 kPa [ln (DIST (m) + 0.1)]

Compaction Levels and Tree Regeneration in Aspen Clearcuts

The regeneration density varied within harvesting treatments (Table 1), ranging from 0 to 76,000 t/ha and plots farthest from the skid trail represented a range from 0 to 15,000 t/ha (Table 1). Regeneration density in the skid trail ranged from 0 to 5,000 t/ha. Maximum regeneration heights ranged from 3.3 to 9.3 m. Plots farthest from the skid trail represented a range of maximum tree height values from 4.1 to 9.3 m (Table 1), and maximum tree heights in the skid trails ranged from 3.7 to 8.7 m.

In summer and winter harvested aspen clearcuts, regeneration density and height were negatively associated with soil compaction. On aspen clearcuts, sites harvested during winter had higher relative total regeneration densities as compared to sites harvested in summer. The magnitude of this effect varied with predicted relative soil compaction as indicated by two robust models, equation 3:

[3] Relative total density = 247 - 1.4(PRED COMP) - 0.1(PRED COMP*SEASON)

where for SEASON, winter = 0 and summer = 1; and equation 4:

[4] Relative total density = 238 - 1.4 (PRED COMP) - 16.1(SEASON)

Note, that on winter harvested sites the density at 100% compaction, i.e., control conditions, is greater than 100%, indicating that plot 5 did not always have the lowest density in a transect. This resulted in an inflated intercept and slope for winter harvested sites (note, the slope is already steeper than the slope for summer harvested sites) and may be partially responsible for having two robust models.

The slope, but not the intercept, of relative maximum height was significantly different, i.e., steeper (p=0.10) for sites harvested in summer versus winter (Equation 5, Figure 4c), indicating that height differences are mainly due to higher sensitivity to compaction after summer harvests:

[5] Relative maximum height = 139 - 0.35(PRED COMP) - 0.03(PRED COMP*SEASON)

Interactive Effects of Residual Basal Area and Soil Compaction on Tree Regeneration

Residual basal areas varied across sites (Table 1), ranging from 0 to 31 m^2/ha. In general, residual basal area negatively impacted regeneration density and growth. The

relative magnitude of this effect did not differ between summer and winter harvested sites, but varied with predicted relative soil compaction as indicated by equation 3:

[6] Relative density = 379 - 2.3(PRED COMP) - 17.5(BA) + 0.1(PRED COMP*BA)

The BA, PRED COMP, and PRED COMP*BA parameters were significant at $p<0.01$ with an adjusted model R-square of 0.21. Figure 5a provides a visual example using this model to predict density at three levels of residual overstory basal area. Again, note that the fact that plot 5 in winter aspen clearcuts did not always have the lowest density inflated the intercept and slope of this model.

To predict maximum regeneration height, a full model containing PRED COMP, BA, and PRED COMP*BA as independent variables was not significant. Investigating these variables individually or in combination as independent variables indicated that the relationships did not differ between summer and winter harvested sites. The model with the highest fit and only significant parameters was:

[7] Relative maximum height = 140 - 0.4(PRED COMP) - 0.005(PRED COMP*BA).

A visual example of this model is presented in Figure 5b.

The alternate method of analyzing effect of residual basal area and soil compaction on regeneration density and height supported the findings described above. The intercept and slope coefficients of regeneration density on predicted soil compaction decreased as residual basal area increased ($p<0.01$). Similarly, the intercept and slope coefficients of maximum regeneration height on predicted soil compaction decreased as residual basal area increased ($p<0.01$).

Aspen Productivity Predictions

For aspen sites clearcuts in winter, areas in skid trails and landings were predicted to produce 83 m^3/ha of volume at age 50 compared to 141 m^3/ha in adjacent areas. This related to a 41% difference in productivity at age 50. For aspen sites with residual basal area of 6 m^2/ha, areas in skid trails and landings were predicted to produce 83 m^3/ha of volume compared to 188 m^3/ha in adjacent areas. This related to a 55% difference in productivity at age 50.

Discussion

Many studies in the Great Lake States conclude aspen suckering occurs at a higher density and with greater height growth when harvest operations take place in the winter months (Weigle and Frothingham 1911, Zehngraff 1946, 1947, Stoeckeler 1947, Stoeckeler and Macon 1956). These authors suggest that likely the higher below ground carbon storage in winter may be responsible for this. Root carbohydrate content is highest in early fall, remains at high levels throughout the dormant season, and is lowest in spring due to leaf flush (Schier and Zasada 1973, Tew 1970). While I could not test this phenomena directly due to confounding factors like age differences between the suckers. I did determine a higher sensitivity of suckers to compaction as evident by the higher density and height reductions on high compaction areas of summer versus winter harvested sites. Significantly fewer seedlings of northern hardwood species have been documented on compacted areas such as skid trails, compared to less compacted areas (Nyland et al. 1977, Moehring and Rawls 1970, Ruark et al. 1982). Furthermore, sites harvested during the winter months have less potential for soil disturbance since the frozen soil is less conducive to damage by harvesting equipment (Mace et al. 1971). Zehngraff (1946) and Bates et al. (1993) cited similar trends of decreased aspen sucker density and height on summer versus winter harvested sites.

My results imply that, in terms of maximizing aspen regeneration, there is a three-fold benefit to harvesting operations in the winter months. Soils are likely frozen,

resulting in lower soil compaction, roots have higher carbon storage, and maybe due a combination of these factors, sprouts are less sensitive to compaction. A recent survey indicates that 54% of all harvesting operations in Minnesota occurred during winter months (Puettmann and Ek 1999), but no information about the proportion of aspen winter harvests exists.

The difficulties in interpreting regeneration density responses are due to the issue that on some transects in the winter harvested sites, the "control" conditions, i.e., plot 5, had lower densities than plots 3 and 4. This may be partially due to measurement errors, e.g., plot 5 may have been closer to another unrecognized skid trail than 15m. Another, more likely alternative is that this result may be a random effect and the sample size was not large enough. Other standardization techniques, e.g., combining the two plots farthest from the skid trail did not produce satisfactory results either. Thus, the analysis of regeneration density has to be viewed cautiously. With "proper" standardization results, i.e., the predicted relative total density at 100%, compaction should be 100%. Thus, the differences between the slopes of the lines for relative total density on summer and winter harvested sites would be enlarged. Thus, even with an inflated intercept and slope the conclusion regarding the higher sensitivity of summer harvests to compaction is valid.

This raises an important question: what are the impacts of soil compaction and residual overstory at rotation age? The answer to this question involves aspects of competition induced mortality, since young aspen stands experience rapid self-thinning. It may be quite likely that the lower density of summer harvested stands leads to lower competition levels that eventually improve individual tree growth (Graham et al. 1963). However, since my study sites are still in the regeneration or early stem exclusion phase (Oliver and Larson 1996), it may be too early to tell whether seasonal differences in regeneration trends will persist throughout the life of these aspen stands. Likewise, many studies cited above indicating seasonal differences in aspen regeneration have only focused on first and second-year trends. Ek and Brodie (1975) produced a suckering model for the Lake States that considers ingrowth, and found winter harvests to produce

17 percent more suckers than summer harvests after two entire growing seasons, but differences between densities decreased over time.

My study set out to answer one question that is discussed frequently among foresters: does soil compaction on and away from skid trails persist or will it be mitigated over time? Even eleven years after harvest I still saw significant differences in soil compaction between skid trails and adjacent areas assumed to have less logging traffic. Holman et al. (1978) found that bulk density levels in areas apart from skid trail returned to precut levels within one year, but within the three years of their study, skid trails in summer cuts had not yet returned to their precut bulk density levels. Stone and Elioff (1998) found significantly greater bulk density and soil strength in compacted areas versus non-compacted areas five years after treatment. Other studies support the notion that soil compaction recovery on skid trails can be a slow process, often taking over 40 years for soil compaction levels on skid trails to resemble precut conditions (e.g. Vora 1988). Consequently, my results indicate that logging traffic should be minimized and concentrated on as few skid roads as possible since the initial machinery passes create the majority of the disturbance (Hatchell et al. 1970, Shetron et al. 1988, Murphy 1982, Shepperd 1993, Williamson and Neilsen 2000). Harvesting machinery can also cause root damage with no apparent soil disturbance, significantly decreasing aspen's regeneration capacity through fine root and suckering root injury and death (Shepperd 1993). Rutting and root damages have been shown to contribute to reduce sucker density (Shepperd 1993) and height growth (Smidt 1996).

Aspen regeneration was affected by the interaction between the amount of residual overstory on a site and the corresponding levels of soil compaction, making avoidance of soil disturbance even more critical in areas with heavy overstory residuals. Again, the actual equations predicting density must be viewed with caution, as the intercept of the relative total density model is inflated due to the standardization issue described above. However, the alternative analysis methods supported the basic conclusions that soil compaction and residual overstory interactively reduce sucker densities. The practice to leave more residuals after a harvesting operation negatively impacts future aspen growth and productivity due to the competition from overstory

trees, and my results are similar to other studies (e.g., Schier and Smith 1979, Stoeckler and Macon 1956, Hove and Blinn 1990, Ffolliott and Gottfried 1991, and Huffmann et al. 1999). Zehngraff (1947) reported lower aspen regeneration density levels 11 years after clearcut (16,877 trees per hectare) than my results showed after an average of 6 growing seasons (16,000 to 30,000 trees per hectare).

More importantly, do these remaining levels of soil compaction on skid trails and negative influences of residual basal area predict future reductions in stand productivity? My results agree with other studies that found compacted areas such as skid trails to contain lower aspen regeneration densities as compared to adjacent uncompacted areas. In some cases even, these regeneration differences persisted throughout the life of a stand (e.g. Bates et al. 1990, Schier et al. 1985, Shepperd 1993, and Stone et al. 1998). Studies looking at future productivity of recently harvested aspen stands agree that to sustain aspen productivity following a harvest, the density and quality of regeneration plays an important role (Navratil 1996). However, unless the sites are not fully captured by aspen, early differences in densities seem to diminish over time (Ek and Brodie 1975). Fully stocked aspen clearcuts to regenerate at high densities, often culminating their productivity between the ages of 50 and 65 years, with optimal total volumes ranging from 200 to 400 m^3/ha (Peterson and Peterson 1992). None of these studies looked at the potentially detrimental effects of soil compaction and residual basal area (e. g. Raile and Hahn 1982, Ek and Brodie 1975).

These productivity decline estimates need to be put in perspective by the actual area they relate to within an aspen harvest, that are compacted as part of the harvesting operation. While the negative impact of soil compaction on regeneration is enhanced in areas with high residual cover, the area impacted by soil compaction is less under partial harvest compared to clearcutting operations. For example, Stokes et al. (1997) found that 13.7 %, 13.2 %, 12.5 %, 9.6 %, and 8.2 % of the stand area are in skid trails after clearcutting, shelterwood, seed-tree, group selection, and single tree selection methods respectively. Additionally, a study by Wert and Thomas (1981) looking at skid road effects on Douglas-fir growth found 10% of their study area to be in skid roads 32 years

after harvest. These numbers seem lower than the values 25 to 30% in skid roads as reported by Gessel (1955), Dryness (1965), and Froehlich (1973).

Based on the results from this study I assumed that higher compaction values related to areas found in skid trails. By applying a conservative approach, there could be the potential for 10% of an aspen clearcut site to contain skid trails, relating to a 4% decline in overall productivity for a winter harvested site. A site with a higher area impacted by harvesting, e.g., 20% of an aspen clearcut contain skid trails, would result in an 8% decline in overall stand productivity. Based on the results of this study, summer aspen clearcuts are more sensitive to soil compaction, and therefore projecting volume estimates becomes even more significant in skid trails of summer cuts. A residual overstory in combination with soil compaction would obviously reduce the productivity on the skid trails, but the overstory would also impact the regeneration in the areas between skid trails.

Therefore, among other factors when designing a timber management plan, foresters must not only consider implications of harvest operations on potential soil compaction, but the potential reduction in site productivity due to the aerial extent of impact.

Conclusions

In summary, my study results indicate that various factors interact in the regeneration of aspen stands. Winter clearcut harvests that take advantage of belowground carbon storage and frozen soil conditions provide better conditions for aspen regeneration. Summer harvests showed higher soil compaction, which may discourage aspen regeneration in spots and increase the opportunity of other species seeding in on the disturbed skid trails, thus allowing a diverse mixture of species to become established. On the other hand, when only aspen are cut, leaving a few residuals after harvest still allows aspen to sucker and dominate the regeneration. However, density and growth of aspen regeneration will be reduced when residual overstory

remains after harvest. Furthermore, increased soil compaction and residual overstory left after harvesting activities can interact and create conditions most detrimental to aspen regeneration. Whether these reductions in regeneration are consequential at the end of a rotation is not fully known and needs to be investigated further.

Table 1. Data for control conditions (plot 5 of transects) in aspen dominated stands separated by sites within harvest type. Values in parentheses are standard deviations. Site index values are for whole site.

			Plot 5 (i.e., control conditions)				
Years Since Harvest	Season of Harvest[a]	Site Index	Residual Basal Area (m^2/ha)	Regen Density (trees/ha) of >2.54 cm DBH	Total Regen Density (trees/ha)	Maximum Regen Height (m)	Median Compaction (kPa)
Aspen Clearcut-Winter (residual BA < 1.0 m^2/ha)							
4	W	23	2 (2.4)	5,500 (2,645.8)	30,500 (18,627.9)	5 (0.5)	3,224 (708.7)
8	W	24	1 (1.0)	9,750 (2,630.0)	16,000 (6,377.0)	7 (1.0)	5,344 (1,848.1)
5	W	23	0 (0)	9,500 (4,654.7)	28,250 (8,732.1)	6 (1.0)	2,924 (649.8)
6	W	23	0 (0.5)	2,000 (1,414.2)	9,500 (7,325.8)	5 (0.3)	4,499 (1,302.9)
6	W	23	0 (0)	5,500 (3,109.1)	35,500 (13,527.8)	6 (1.1)	6,423 (1,558.2)
11	W	23	0 (0)	8,750 (2,872.3)	25,000 (13,114.9)	8 (0.6)	4,849 (2,151.2)
11	W	15	0 (0)	5,000 (4,242.6)	23,750 (14,174.5)	5 (0.6)	2,374 (833.9)
Aspen Clearcut-Summer (residual BA < 1.0 m^2/ha)							
6	S	24	1 (1.3)	4,250 (2,630.0)	-	6 (0.7)	1,675 (206.1)
7	S	24	0 (0)	8,250 (2,630.0)	29,500 (17,000.0)	9 (0.9)	3,712 (2,384.2)
6	S	24	0 (0.5)	7,500 (2,886.8)	22,500 (7,852.8)	7 (0.8)	925 (150.0)
5	S	26	1 (1.0)	3,000 (2,828.4)	31,750 (13,696.1)	5 (0.7)	3,861 (2,727.3)
7	S	23	0 (0)	7,000 (4,966.6)	-	7 (0.7)	1,250 (288.6)
4	S	20	0 (0.5)	4,000 (3,162.3)	64,000 (8,756.0)	5 (0.7)	3,424 (1,693.4)
Aspen Cut w/ Low Residual Overstory (residual BA = 3 ± 3.4 m^2/ha)							
6	S	24	6 (2.4)	8,500 (4,795.8)	-	8 (0.6)	1,150 (147.2)
5	S	21	1 (0.8)	7,000 (3,741.7)	-	6 (0.3)	3,812 (753.0)
4	W	23	2 (1.6)	4,250 (2,217.4)	-	6 (0.8)	3,737 (1,387.3)
5	S	22	8 (4.8)	1,000 (8,16.5)	-	5 (0.3)	4,249 (932.5)
6	W	25	4 (3.4)	6,750 (2,362.9)	-	6 (0.4)	6,298 (787.2)
6	W	24	2 (1.6)	7,500 (4,434.7)	-	6 (1.3)	4,799 (803.9)
Aspen Cut w/ Heavy Residual Overstory (residual BA = 12 ± 8.1 m^2/ha)							
5	S	21	5 (1.5)	2,250 (1,893.0)	-	5 (0.4)	2,381 (372.6)
6	W	20	18 (9.1)	250 (500.0)	-	6 (0)	550 (343.9)
6	S	21	18 (8.7)	1,250 (2,500.0)	-	6 (0)	1,968 (350.7)
7	W	22	18 (2.2)	0 (0)	-	-	1,125 (525.1)
6	W	15	4 (4.6)	6,750 (4,991.7)	-	8 (0.3)	2,066 (907.1)
6	S	17	15 (2.6)	3,000 (4,242.6)	-	7 (0.9)	1,112 (265.7)

[a]Season of Harvest: W=winter, S=summer

Table 2. Study site averages for aspen dominated stands separated by harvest type. Values in parentheses indicate standard deviation.

Harvest type	Residual Basal Area (m^2/ha)	Proportion of regeneration (%) that was aspen	Regeneration Density (trees/ha) of >2.54 cm DBH	Total Regeneration Density (trees/ha)	Maximum Regeneration Height (m)	Median Compaction (kPa)
Aspen Clearcut-Winter	<0 (0.8)	97	3,808 (3,644.5)	21,963 (19,280.4)	6 (1.3)	3,120 (1,991.0)
Aspen Clearcut-Summer	<0 (1.1)	97	4,143 (3,922.9)	18,643 (16,843.4)	6 (1.4)	4,494 (2,030.5)
Aspen Cut w/ Low Residual Overstory	3 (3.4)	99	3,758 (3,953.5)	-	6 (1.1)	4,152 (1,795.5)
Aspen Cut with Heavy Residual Overstory	12 (8.1)	95	1,842 (3,466.5)	-	6 (1.4)	1,904 (1,107.8)

Figure 1. Aspen dominated study site locations in Minnesota.

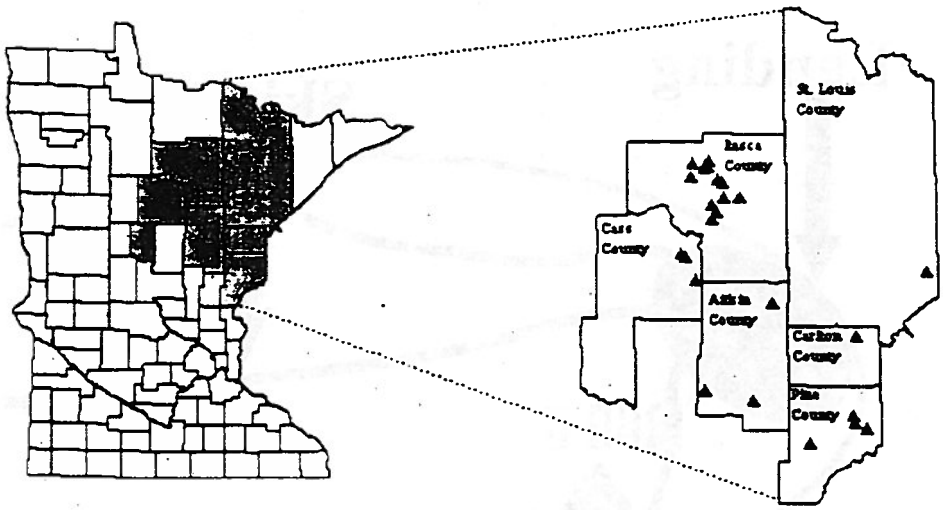


Figure 2. Regeneration plot layout within aspen dominated study sites. Five regeneration plots were placed along four transects per site, comprising twenty regeneration plots to investigate patterns of aspen regeneration following harvest.

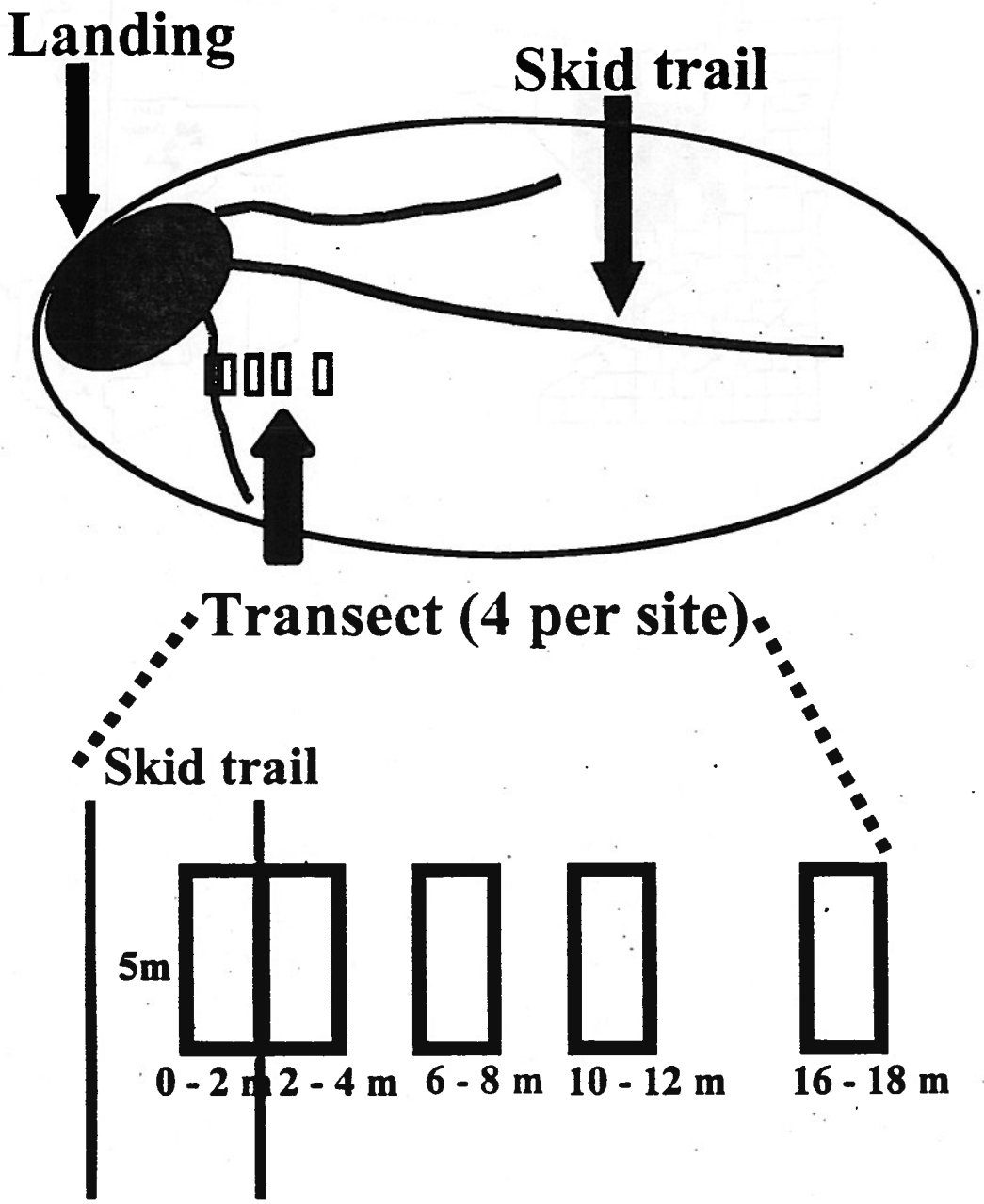


Figure 3. Relative soil compaction levels in summer vs. winter aspen clearcuts as a function of distance from skid trail.

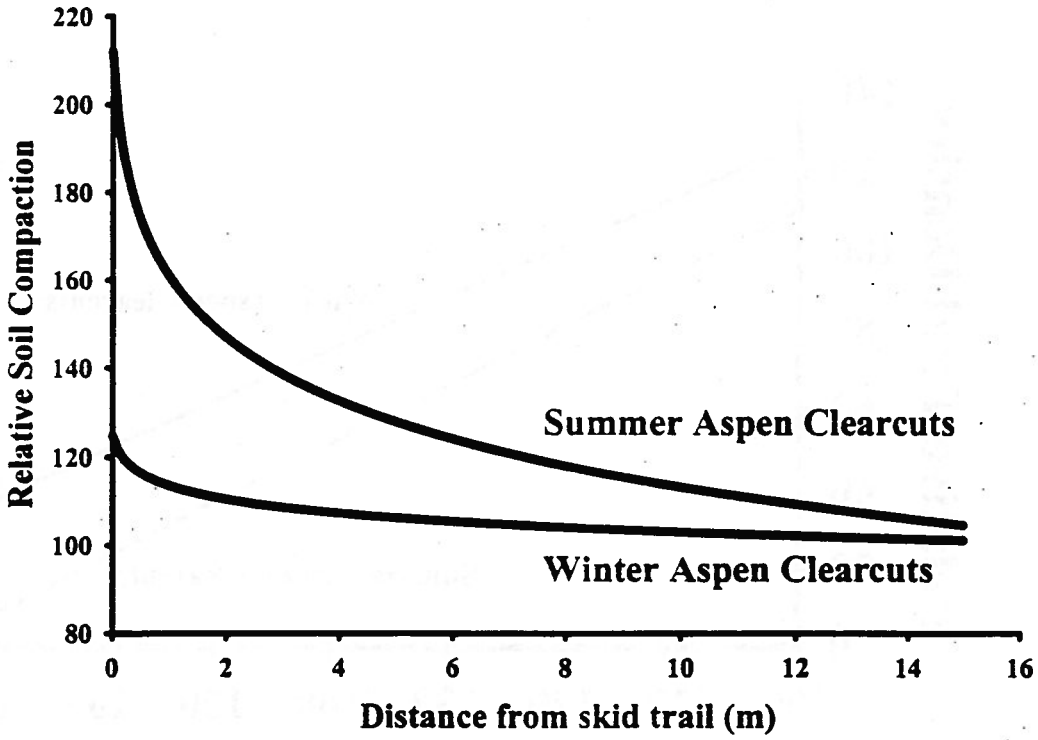


Figure 4 a. Predicted relative soil compaction versus relative total regeneration density by season of harvest (see equation 3) for aspen clearcuts. Note, that intercept is at 100% predicted compaction, i.e., control conditions.

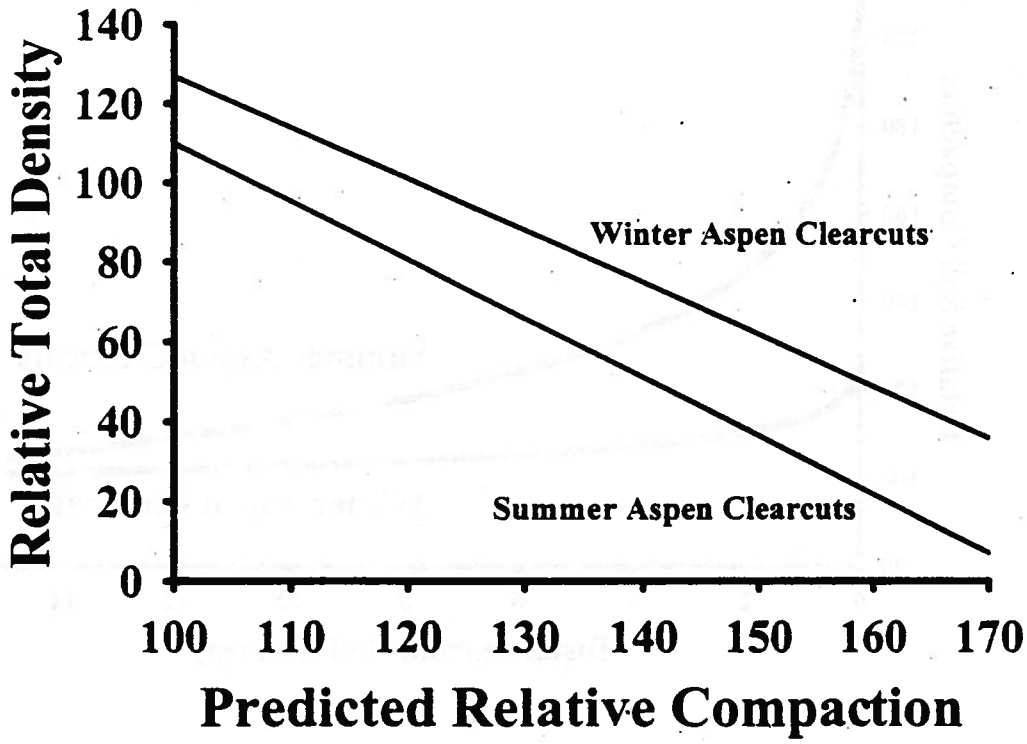


Figure 4 b. Predicted relative soil compaction versus relative total regeneration density by season of harvest (equation 4) for aspen clearcuts. Note, that intercept is at 100% predicted compaction, i.e., control conditions.

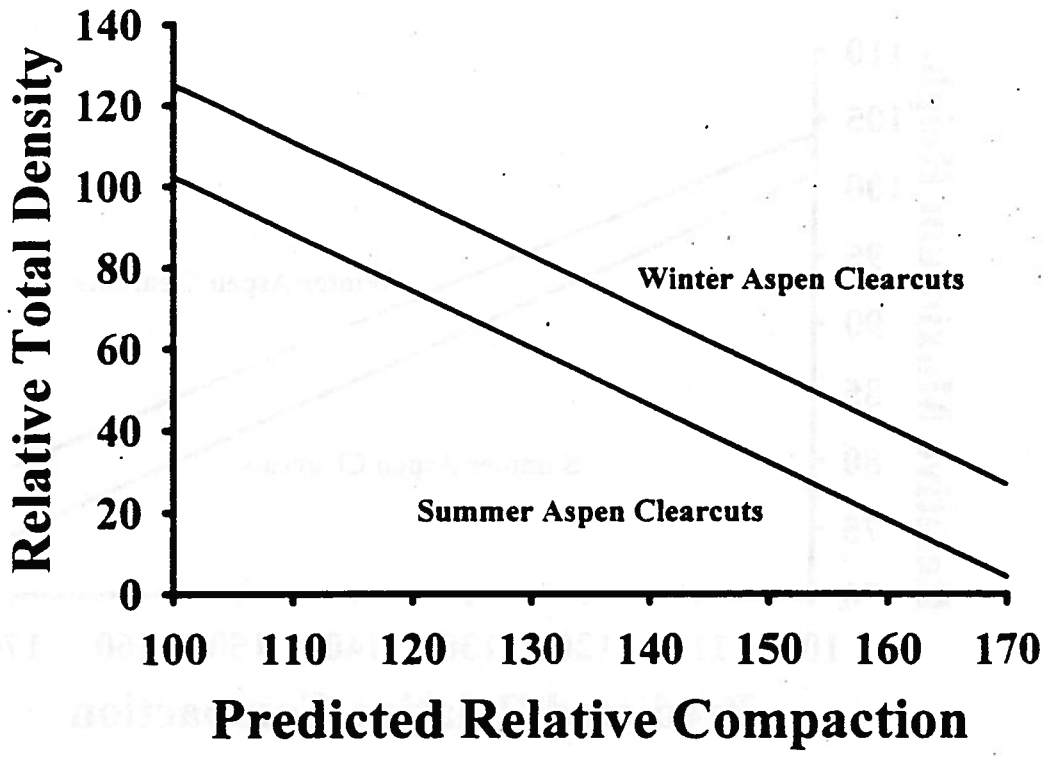


Figure 4 c. Predicted relative soil compaction versus relative maximum regeneration height by season of harvest (equation 5) for aspen clearcuts. Note, that intercept is at 100% predicted compaction, i.e., control conditions.

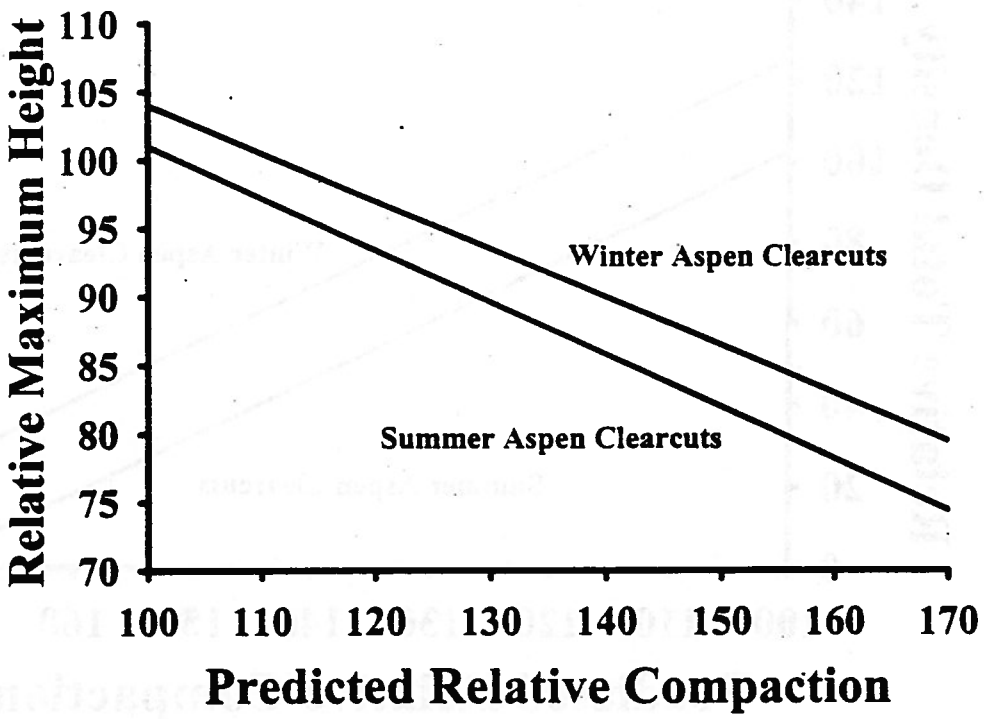


Figure 5 a. Predicted relative soil compaction versus relative regeneration density according to three levels of residual basal area. Equation 6 was used to determine interactive effects of soil compaction and residual basal area on aspen density response. Note, that intercept is at 100% predicted compaction, i.e., control conditions.

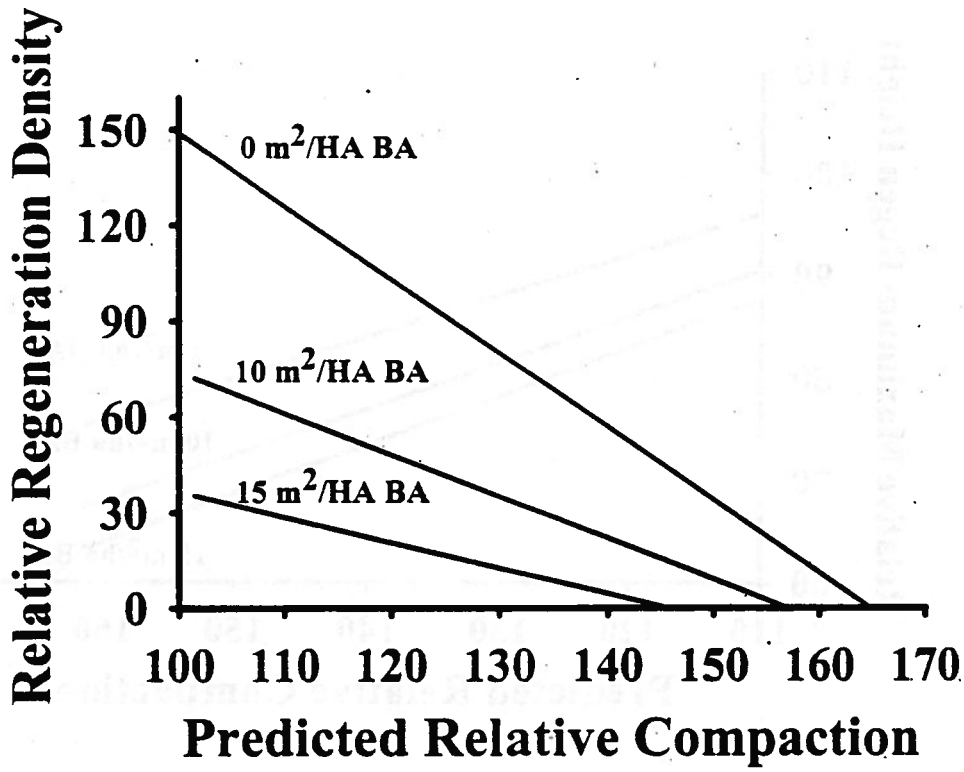
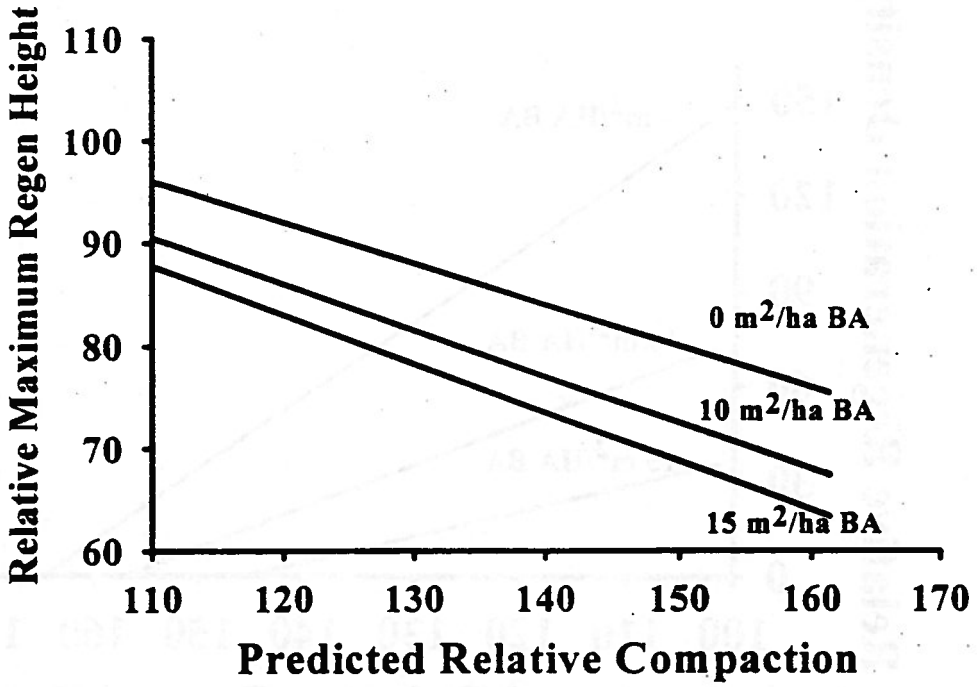


Figure 5 b. Predicted relative soil compaction versus relative maximum regeneration height according to three levels of residual basal area. Equation 7 was used to determine interactive effects of soil compaction and residual basal area on aspen height response. Note, that intercept is at 100% predicted compaction, i.e., control conditions.



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Chapter 3

Residual forest canopy and soil disturbance influences on tree regeneration in Northern Hardwood stands: A literature review

Introduction

Natural and human-induced disturbances alter the dynamics of northern forest ecosystems, and perpetually modify a landscape. Silvicultural systems attempt to modify stand characteristics by simulating natural disturbance regimes, therefore influencing stand density and composition of post-harvest vegetation. Forest managers must evaluate how disturbances impact stand development, how they interact with vegetation composition, and then incorporate these considerations into the planning process. Forests of the Great Lakes region, specifically of Minnesota, provide opportunities to investigate disturbance patterns and the potential for management objectives to modify stand characteristics. White pine (*Pinus strobus* L.), red pine (*P. resinosa* Aiton.), jack pine (*P. banksiana* Lambert.), northern hardwood species (e. g. sugar maple (*Acer saccharum* Marsh.), paper birch (*Betula papyrifera* Marsh.), basswood (*Tilia americana* L.), and aspen (*Populus spp.)* largely dominated pre-settlement timberlands of Minnesota and the Lake States (Ahlgren and Ahlgren 1983, Curtis 1959). During the 1830's to 1900's, the timber industry expanded, resulting in the logging and subsequent burning of many red and white pine forests. The decline of once dominant pine forests provided an opportunity for aspen to expand its dominance. Fire suppression in historically pine dominated stands also provided an avenue for compositional shifts to a larger hardwood component (Host et al. 1987). Increased timber harvesting also influenced northern hardwood stand composition in instances where selective hardwood harvests took place (Ahlgren and Ahlgren 1983). Due to only partial harvests of hardwood species, northern hardwood stands have mostly retained their tree species densities and diversities (Curtis 1959).

Timber species comprising the northern hardwood ecotype provide significant proportions of the Lake States' forest harvest. In addition to their value as a timber resource, hardwoods are also valued for aesthetic, recreational, and wildlife purposes. In the Lake States, research and management objectives for northern hardwood types traditionally concentrated on single tree and group selection (Tubbs 1977). The species comprising a northern hardwood stand differ in their growth rates and shade tolerances,

making stand analysis, management prescription, and silvicultural implementation more difficult than in pure aspen stands. Furthermore, many uneven-aged northern hardwood stands present a greater complexity of regeneration issues not encountered in vegetatively regenerated even-aged stands. Over the last four decades, hardwood managers and researchers have increased application of even-aged practices to enhance their options for harvesting efficiency, stand maintenance, compositional shifts, and multiple use factors (Nyland 1986, Wang and Nyland 1996). Although modifying density through harvest regimes achieves control on future regeneration of forest stands, the negative effects of site disturbance must also influence a management plan. This paper focuses on the ecology of northern hardwood stands, the influence management options have on hardwood ecosystems, and the interacting effects of environment and management on future stand composition.

Ecology of Northern Hardwood Tree Species

Northern hardwoods (excluding aspen) comprise roughly one-third of Minnesota's timberland with most of these stands located in the central and southeastern sections of the state (Miles et al. 1995). Main species composing Minnesota's northern hardwood forests include sugar maple (*Acer saccharum* Marsh.), basswood (*Tilia americana* L.), northern red oak (*Quercus rubra* L.), red maple (*A. rubrum* L.), paper birch (*Betula papyrifera* Marsh.), yellow birch (*B. allegheniensis* Briton), green ash (*Fraxinus pennsylvanica* Marsh.), black ash (*F. nigra* Marsh.), and ironwood (*Ostrya virginiana* (Mill.) K. Koch); with smaller associations of trembling aspen (*Populus tremuloides* Michx.), bigtooth aspen (*P. grandidentata* Michx.), white oak (*Q. alba* L.), bur oak (*Q. macrocarpa* Michx.), and American elm (*Ulmus americana* L.).

The majority of northern hardwood forests contain long-lived tree species which at advanced stages, respond positively to overstory release (Tubbs 1977). Under the right conditions, most hardwood species have the potential to regenerate prolifically by seed, and vegetatively regenerate from stump sprouts. Some species of hardwoods regenerate well under heavy overstory shade, while others are shade intolerant and require canopy

gaps or clearings to survive. Several species such as yellow and paper birch experience enhanced survival and germination on recently disturbed seedbeds (Marquis 1965). Due to these variations in its component species' ecology, the northern hardwood forest presents managers with a diversity of silvicultural options. Among other factors, deciding what level of overstory removal should be left after a harvest depends on landowner objectives, site-specific environmental variables, species' competitive abilities, and pre- and post-harvest conditions.

The factor most limiting to the initiation and growth of tree seedlings may be the amount of light reaching the forest floor (Canham 1988, Kobe et al. 1995, Walters and Reich 1996). Different species experience a trade-off in their competitive abilities; shade tolerant species generally grow slowly and efficiently in low light where intolerants may die of suppression (Canham 1985, Canham 1989, Kobe et al. 1995). In the absence of major disturbances, shade tolerant species eventually replace intolerants. Alternatively, intolerant species can dominate exposed areas where they are able to grow faster and at least in the short term, outcompete shade tolerant species (e. g. Kobe et al. 1995, Marks 1975, Runkle 1981, Hibbs 1982, Canham and Marks 1985). Some shade tolerant species may survive in the understory of exposed areas though or seed in, and can eventually replace pioneer intolerant species. These mechanistic differences in shade tolerance as a response to gap dynamics largely drive forest succession (Barnes et al. 1998, Walters and Reich 1997). Species community structure shifts along gradients of gap size (McClure and Lee 1993) depending on the disturbance and competitive strategies of pre- and post-harvest vegetation. Phillips and Shure (1990) found tree species richness to increase along a gradient of increasing gap size. Tree species of Minnesota's northern hardwood forest ecosystem display these variations in shade tolerance, and in turn respond differently to gradients of overstory release.

Scientific studies investigate species specific competitive strategies which managers can then extrapolate to make implications for many different ecosystem types. Sugar maple is among the most shade tolerant species, and it commonly dominates in late successional sites on better soils (Curtis 1959, Walters and Reich 1997, Host et al. 1987).

Red maple also tolerates shade and it responds well to disturbance or thinning (e. g. Trimble 1974, Marquis 1969, Strong and Erdmann 2000, Lorimer 1980, Miller 1997, Palik and Pregitzer 1992) based on its ability to exploit higher resource levels (Tift and Fajvan 1999). Erdman et al. (1985) found younger red maples to put on up to 70% greater diameter growth 7 years following thinning. In general, oaks are less shade tolerant than maples, and exhibit enhanced growth following overstory release (Larsen et al. 1997, Allen and Marquis 1970, Clatterbuck et al. 1999). Several studies suggest however, that under complete overstory removal, i.e. clearcuts, oak seedlings regenerate but may be outcompeted by more successful intolerant species (O'Hara 1986, Ward and Stephens 1999). Other studies point out the decline in oak-dominated ecosystems due to their poor ability to outcompete more shade tolerant species such as red maple (Lorimer 1984, Beck and Hooper 1986). To successfully maintain species diversity and adequate stocking levels, it is often important to consider these species-specific differences in regards to shade tolerance. In addition to its competitive abilities, a tree's regeneration success depends on stand level properties that may or may not be under a manager's control, such as site quality and parent stand composition.

Silvicultural manipulations of a forest stand often attempt to simulate natural patterns of disturbance to achieve certain management objectives. Studies indicate that hardwood thinnings increase crop-tree basal area and diameter growth of tolerant and some intolerant seedlings along a gradient of increasing residual basal areas (Marquis 1969, Greene et al. 1999, Allen and Marquis 1970, Miller 1997, Minckler and Woerheide 1965). In contrast, other research finds near to complete overstory removal enhances tree survival and growth, most commonly for shade intolerants and intermediates (Myers and Buchman 1988, Walters and Nyland 1989). The overstory composition and degree of basal area removal can shift species distributions to a desirable composition of high value species, (Wang and Nyland 1993, Marquis 1967) or undesirable composition of low quality competition species (Bjorkbom and Walters 1986). The presence of advance regeneration is often considered to be the critical factor that determines future stand composition (Larsen et al. 1997, Bjorkbom and Walters 1986, Greene et al. 1999). Wang and Nyland (1993) found that following a hardwood clearcut, advance seedlings and

stump sprouts contribute to the regeneration of both tolerant and intolerant tree species. To maintain silvicultural control over future stand composition, land managers manipulate both residual canopy and advance regeneration densities.

Harvesting Impacts on Northern Hardwood Stands

The degree of site disturbance a harvest activity creates depends on several factors such as level of overstory removal, season of harvest, skid trail layout, soil texture and moisture content, slope, aspect, and damage to advance regeneration and residuals. Intensity of harvesting can be characterized by the amount of overstory removed and by its effects on post-harvest stand vegetation. A clearcutting regime removes most or all of the existing overstory and may reduce survival of advance regeneration by creating a harsh environment. As stated before, in harvested stands where shade tolerant species previously inhabited a stand, under these conditions future composition may shift to favor early successional, shade intolerant species (Canham 1985, 1989, Kobe et al. 1995). Larsen et al. (1997) found oaks to regenerate best under low residual basal areas of less than 14 m^2/ha. Strong and Erdmann (2000) found similar results for red maple saplings responding with 2.5 times the diameter growth under a residual canopy of 9.2 m^2/ha as compared to under the control stand with a residual canopy of 27.2 m^2/ha. Conversely, limited overstory removal may shade and inhibit regeneration of desired shade intolerants (e. g. Kobe et al. 1995, Marks 1975, Runkle 1981, Canham and Marks 1985).

Although various species respond differently along a gradient of overstory removal, and some tree species respond positively to site disturbance that creates optimal seedbed conditions; severe soil disturbance inhibits regeneration of most northern hardwoods. Harvest machinery traffic creates a skid trail system resulting in soil compaction that may significantly influence tree regeneration and represents another factor that can be used to characterize site damage. The section on aspen regeneration (Chapter one) covers these issues in far greater depth, but it also applies to northern hardwood regeneration. Season of harvest influences the success of regeneration, for there is likely less damage to fine root systems when soils are frozen. As stated

previously in Chapter one, soil bulk density reflects the gradient of soil compaction created from harvest activities. Several studies revealed significantly fewer seedlings on compacted areas such as skid trails, compared to less compacted areas (Nyland et al. 1977, Moehring and Rawls 1970, Ruark et al. 1982, Corns 1988). Alternatively, several northern hardwood species respond positively to soil disturbance. Marquis (1965) found higher densities of paper and yellow birch in disturbed, skid trail areas as compared to adjacent, non-skid trail areas.

The differences between aspen and hardwood ecology reflect their different susceptibilities to soil compaction. Aspen respond vigorously to harvesting by root and sometimes stump sprouting. Nearly all northern hardwood species exhibit sprouting abilities, but also rely on advance reproduction, seed dispersal from residuals, and seed bank stores for future stand composition. Site disturbance can also discourage survival of advance regeneration and residual overstory trees by removing smaller diameter individuals and damaging trees left on a site. In order to measure the magnitudes of site disturbance effects on future stand composition and density, researchers employ several different methodologies listed in the next section.

Quantifying Future Hardwood Stand Composition and Productivity

Foresters may rely on pre-existing stand data as well as post-harvest outcomes to make silvicultural prescriptions, assess the outcome of a certain management regime, and to predict impacts on future stand structure and composition. As a measure of the amount of residual forest canopy resulting from a harvest regime, basal area commonly indicates potential overstory effects on post-harvest vegetation (Greene et al. 1999). Other studies consider percent canopy cover a better representation of the degree of residual shading on regenerating stands (Huffmann et al. 1999). Managers also consider the potential influence of overstory composition on understory vegetation. To assess site damage from harvesting operations, soil compaction helps characterize the degree of traffic damage. Soil bulk density samples indicate levels of compaction, as do instruments that measure a soil's resistance to penetration, e. g. soil cone penetrometers. Describing vegetation

response along a gradient of soil compaction provides forest managers with valuable information regarding the impact of harvest operations.

Species composition by percent cover commonly describes the status of understory forest vegetation. Assigning a percent cover value to existing vegetation indicates the degree of dominance each species contributes to current stand composition. By dividing stand components into height strata, foresters can then examine species diversity among the regeneration vegetation (understory), advance regeneration (midstory), and residual overstory. Among all other factors listed previously in this chapter, understory and midstory compositional analyses then help to determine the degree to which overstory basal area removal influences individual species' competitive strategies. Quantifying the effects of human-induced disturbance regimes allows forest managers to investigate the patterns of silvicultural manipulation that successfully alter forest stand dynamics, and to predict future patterns of development and productivity.

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Chapter 4

Residual forest canopy and soil disturbance influence tree regeneration in Northern Hardwood stands

Abstract

Impacts of clearcutting and partial harvest operation in northern hardwood stands were examined at 15 study sites in northern Minnesota. In each stand, tree regeneration and advance regeneration composition, residual overstory, and soil compaction were determined on landings, skid trails and areas off skid trails in the summers of 1997 and 1998, 4 to 8 years after harvest. Leaving more residual basal area was associated with lower soil compaction, and resulted in shade tolerant species composing a larger proportion of the regeneration. My results show the importance of understanding complex interactions between pre-harvest and post-harvest conditions, harvesting disturbance, and soil properties as they determine future stand composition and productivity.

Additional Key Words:

Northern hardwoods, tree regeneration, shade tolerance, residual forest canopy, forest soil compaction, advance regeneration

Introduction

Silvicultural systems attempt to modify stand characteristics by controlling stand density and composition of post harvest vegetation. Forests of the Great Lakes region, specifically of Minnesota, provide opportunities to investigate vegetation responses to disturbance patterns and management objectives aimed at modifying stand characteristics. Since the timber industry expansion of the 1830's to 1900's, studies have shown increasing areas of northern hardwood forests in Minnesota, with shifts in species composition resulting mainly from human-induced disturbance regimes (Widmann and Schmidt 1997). Research and management objectives for northern hardwood forests typically include harvests along the entire gradient of overstory removal, from single tree selection to clearcutting. Over the last four decades, hardwood managers and researchers have increased application of even-aged practices to enhance options for harvesting efficiency, stand maintenance, compositional shifts, and multiple use factors (Tubbs 1977).

The majority of northern hardwood forests contain long-lived tree species that regenerate prolifically by seed and vegetatively from stump sprouts (Tubbs 1977). Hardwood species (excluding aspen) comprise roughly one-third of Minnesota's timberland with most of these stands located in the central and southeastern sections of the state growing on sandy and silt loams (Miles et al. 1995). Main species composing Minnesota's northern hardwood component include sugar maple, basswood, northern red oak, red maple, paper birch, yellow birch, green ash, black ash, and ironwood (Table 2).

In a forest understory, light may be the single most important limiting factor determining initiation and growth of tree seedlings (Canham 1988, Kobe et al. 1995, Walters and Reich 1996, Walters and Reich 1997). Timber harvesting and its associated removal of overstory create gaps in the canopy that allow increased levels of light to reach the forest understory and differentially influence trees and other plant species according to their shade tolerance. Species experience a trade-off in their competitive abilities; shade tolerant species generally grow more slowly and efficiently in low light

where intolerants may die of suppression (Canham 1985, 1989, Kobe et al. 1995). In the absence of major disturbance, tolerant species eventually replace intolerant species, while intolerant species are able to dominate exposed areas (e. g., Kobe et al. 1995, Marks 1975, Runkle 1991, Hibbs 1982, Canham and Marks 1985). These mechanistic differences in shade tolerance largely drive forest succession (Barnes et al. 1998, Walters and Reich 1997).

Harvesting Impacts on Northern Hardwood Stands

The degree of site disturbance a harvest regime creates depends on several factors including the level of overstory removal, damage to advance regeneration and residuals, skid trail layout, and season of harvest. Partial harvests may result in increased diameter growth of the residual trees (Marquis and Ernst 1991, Miller 1997), and diameter growth of tolerant seedlings may be improved more so than that of intolerant seedlings (Marquis 1969, Greene et al. 1999, Allen and Marquis 1970, Miller 1997, Minckler and Woerheide 1965). Other studies show enhanced understory tree seedling survival and growth under low levels of residual basal area, more so for intolerant and intermediate species (Myers and Buchman 1988, Walters and Nyland 1989). Even in clearcut stands that were dominated by tolerant species, composition may shift to favor early successional, intolerant species (Canham 1985, Canham 1989, Kobe et al. 1995). Conversely, high densities of residual overstory may shade and inhibit regeneration of desired intolerant species (e.g., Kobe et al. 1995, Marks 1975, Runkle 1981, Canham and Marks 1985).

During phases with limited or no disturbance, northern hardwoods rely on seed as a means of regeneration. However, after a disturbance such as harvesting, seed dispersal from residuals, soil seed bank, and advance reproduction contribute to the makeup of the future stands. In addition, after death of overstory trees or advance regeneration, sprouting can become a dominant mode of regeneration (Johnson et al. 1997, Larsen et al. 1997). Harvesting operations also reduce survival of advance regeneration and residual overstory trees by direct harvest damage (Bragg et al. 1994, Howard 1996, Reisinger and Pope 1991) or altered growing conditions (Tucker and Emmingham 1976).

Despite variations in tree regeneration response to overstory removal according to shade tolerance, regeneration of northern hardwood species decreases with severe soil compaction (Moehring and Rawls 1970, Nyland et al. 1977, Kochenderfer 1977). Alternatively, species that regenerate best on exposed mineral soil, such as birch species, can be favored by soil disturbance. For example, Marquis (1965) found higher densities of paper and yellow birch in disturbed, skid trail areas of exposed mineral soil as compared to adjacent, non-skid trail areas.

Harvesting machinery traffic creates a skid trail system and results in soil compaction that may influence tree regeneration. Impacts of soil compaction are sometimes difficult to separate from influences of open canopy conditions, because these two variables are correlated. For example, landings are usually heavily compacted and have no residual canopy cover while other portions of the stand may have endured less harvesting activity, resulting in higher residual canopy cover and lower soil compaction. These factors may result in significantly fewer seedlings and sprouts on compacted areas such as skid trails, compared to less compacted areas (Nyland et al. 1977, Moehring and Rawls 1970, Ruark et al. 1982). Another confounding factor influencing regeneration is season of harvest. There is less soil disturbance and compaction when soils are frozen (Mace 1971). Lower soil compaction and greater belowground carbon storage may also influence seasonal variation in sprouting response of hardwood trees. Chapters one and two cover these and other related issues in greater depth; they can also be applied to northern hardwood regeneration.

Although modifying density through overstory removal influences future regeneration of forest stands, the negative effects of associated site disturbance can also influence vegetation response to harvest regimes. This paper investigates the response of northern hardwood forests to different harvesting operations by quantifying the interacting effects of overstory competition and altered seedling environment and soil compaction on future stand composition. The first hypotheses tested that soil compaction levels on skid trails and landings are greater than in areas away from skid trails (Hypothesis 1a), and that summer harvests result in higher soil compaction levels than

winter harvests (Hypothesis 1b). The second hypothesis tested that the proportions of shade tolerant versus shade intolerant species shift between areas away from skid trails, and areas on skid trails and landings. The third hypotheses tested that the interacting effects of increased soil compaction and increased residual basal area negatively influence both tolerant and intolerant regeneration (Hypothesis 3a); and that the effects of increased residual basal area are positively correlated with intolerant advance regeneration and negatively correlated with tolerant advance regeneration (Hypothesis 3b).

Methods

Study Area and Site Selection

This study encompasses 15 northern hardwood forest stands in five counties of northeastern Minnesota (Figure 1, Table 1). These stands were clearcut or partially harvested between 1990 and 1994. I examined impacts of forest practices in the summers of 1997 and 1998, four to eight growing seasons after harvest. Study sites have an average slope of eight percent. The overall mean annual temperature for the study region ranges from 3.8 to 5.6° C (39-42° F), and the overall mean annual precipitation ranges from 66 to 76 cm (26-30 inches) (Anderson et al. 1996). The study sites exist mainly on till parent materials (Anderson et al. 1996). Field data collection methods described in Chapter 2 provided soil texture, indicating that all study sites are located on similar classes of sandy loams and silt loams.

Sites were selected to assure a range of treatment conditions, but fairly homogeneous within-site characteristics and sites covered a gradient of overstory removal, from hardwood clearcuts (0 m^2/ha of residual basal area) to single tree hardwood thinnings (26 m^2/ha of residual basal area) (Figure 1). Sites were only selected if there were no recent major disturbances or management practices since the harvest.

Study Site Properties

I obtained timber sale maps from the United States Forest Service, Minnesota Department of Natural Resources and several counties in northern Minnesota, from which I then chose target locations for subsequent field measurements. Sites investigated in this study comprised an average area of 10.3 ha, ranging from 2 to 15.8 ha and had an average 50 year site index of 18 m taken from the dominant tree species (Table 1); and regeneration age ranged from 4 to 8 years, with a mean of 6 years. I attempted to keep site quality and other site characteristics constant across study sites.. Analyses showed that time since harvest, site index, and soil texture differences between study sites were not a significant contribution in any of the models tested ($p<0.05$).

Sugar maple, northern red oak, and basswood were the most common of the 25 species of residual trees encountered on hardwood study sites, and composed 84 percent of the overstory residual basal area. Red maple, yellow birch, and white birch composed 10 percent of the residuals. The remaining residuals were small components of trembling aspen, bigtooth aspen, green ash, and black ash. Sugar maple and paper birch composed 62 percent of the regeneration tree vegetation, with northern red oak, ironwood, and red maple comprising 19 percent. Sugar maple and northern red oak composed 60 percent of the advance regeneration tree species, along with smaller components of red maple, trembling aspen, basswood, paper birch, and bigtooth aspen comprising 31 percent. These definitions of regeneration and advance regeneration vegetation are defined in greater detail in the next section. Species composition according to study site did not differ significantly along a gradient of residual overstory basal area, but did suggest differential patterns in regeneration and advance regeneration composition (Table 1).

Field Collection and Description of Data

Forest Soil

As an indicator of soil compaction I measured the penetration resistance of the soil matrix using an Eijkelkamp soil cone penetrometer (Bennie and Burger 1988). Resistance to penetration (kPa) was measured in each regeneration plot up to a 15 cm soil depth (ASAE 1990). Force exerted on the penetrometer equaled a uniform rate of approximately 30 mm/sec or slower, and readings were taken at the moment when the cone reached a 15 cm soil depth. A 1 cm^2 base area cone was used on all but 2 study sites. Penetrometer measurements for the two study sites on which a 2 cm^2 base area cone was used were then converted by the following formula:

$$\text{Cone resistance} = \frac{\text{gauge reading}}{\text{base area of cone (cm}^2\text{)}}$$

A minimum of ten randomly selected samples per plot was measured. The measurements on a given study site were taken within the same day to ensure that soil moisture conditions were relatively uniform for an entire site. Readings were ignored when it was obvious that the penetrometer hit a rock or a log, and those readings were not recorded. Although the mean and median penetrometer values for each regeneration plot were correlated by an r^2 value of 0.99, I used the median value to minimize effects of insignificant outlying values.

Ten texture samples were taken from five randomly located points within each study site. For each point, one sample was taken from the 0-25 cm profile, and one sample was taken from the 26-50 cm profile. Texture analysis was conducted in the lab in fall 1998/winter 1999 using a modified hydrometer method (Grigal 1973)

Forest Vegetation

On each study site I placed five, 60 m^2 (0.006 ha) relevé plots, employing the method described in Mueller-Dombois and Ellenburg (1974). Excluding any bladed areas or log piles, one square (7.75 x 7.75 m) relevé was placed on or adjacent to the landing site ("L" plots) to represent the highest disturbance in the stand associated with the lowest levels of residual basal area. Two rectangular (3 x 20 m) relevés were placed within skid trails ("S" plots), representing intermediate disturbance residual basal areas, and two square relevés were placed away from ("A" plots) any landings or skid trails, representing areas of the lowest disturbance and highest levels of residual basal area (Figure 2). All plots were a minimum of 20 meters apart.

To quantify composition of tree regeneration, I separated tree composition into two height strata; "regeneration" or understory (0 - 2 m) and "advance regeneration" or midstory (2 - 10 m). Tree species composition was quantified by making cover estimates by species for all trees located within the relevé in the two separate height strata using the following cover class codes: (1) 1% (single occurrence), (2) <5% (occasional), (3) <5% (plentiful), (4) 5-25%, (5) 25-50%, (6) 50-75%, and (7) 75-100%. For analysis purposes I designated percent cover as the median value of each cover class. It was possible for a single height stratum to contain >100 percent cover due to overlapping layers of vegetation. Therefore, I transformed the data to establish an upper bound value on percent cover. The highest percent cover value in a single height stratum became 100%, and the remaining percent cover values were divided by the absolute highest percent cover value.

Tree species were divided into two categories: shade tolerant and shade intolerant species (Table 2). Tree species were designated as "tolerant" if Burns and Honkala (1990) define them to be very tolerant to midtolerant. "Intolerant" tree species were designated as such, if Burns and Honkala (1990) considered them very intolerant to slightly midtolerant (i.e. *Pinus strobus* L. and *Betula alleghaniensis* Britton).

Residuals were defined as those trees left standing after harvest with a minimum DBH of 18 cm. I measured residual overstory basal area from the center of each relevé plot using a 1-meter factor prism. Residual trees considered "in" were recorded and separated by tree species, considered separately from any regeneration or advance regeneration trees.

Data Analysis

I conducted all statistical analyses using JMP 3.1.6.2 (SAS Institute Inc. 1996). Unless otherwise noted, relationships were considered significant if $p \leq 0.05$. In order to conduct these statistical analyses, I transformed the percent cover data to meet assumptions made in ANOVA and regression analysis by using the arc sine square-root transformation to stabilize variance (Sabin and Stafford 1990).

To quantify impacts of harvesting on soil compaction (Hypothesis 1a), I used one-way ANOVA to compare median compaction values between L, S, and A plots with the Tukey-Kramer HSD procedure (since samples sizes were unequal) (Sokal and Rohlf 1995). I also used the Tukey-Kramer HSD procedure to compare absolute mean compaction values between summer and winter harvested sites (Hypothesis 1b).

To quantify the different levels of percent regeneration cover according to shade tolerance classes (Hypothesis 2), I used one-way ANOVA to compare cover values between L, S, and A plots with the Tukey-Kramer HSD (meeting the same assumptions as described for Hypotheses 1a and 1b).

I investigated the effects of residual overstory and soil compaction and their interactions on regeneration (Hypothesis 3a) and advance regeneration (Hypothesis 3b) composition by fitting regression models. These regression models predicted percent composition as a function of residual basal area, median soil compaction, and residual basal area times median soil compaction and testing the parameters for significance ($p > 0.10$). I used analysis of covariance to determine whether these relationships differed

between shade tolerance classes of the regeneration and advance regeneration. The full models contained indicator variables for shade tolerance on the intercept and slope parameters while reduced models only included indicator variables on either the slope, the intercept, or neither.

Results

Compaction Levels and Timing of Harvest

Median penetrometer values ranged from 800 to 7,000 kPa. Penetrometer readings on landings and skid trails ranged from 800 to 7,000 kPa, and ranged from 800 to 4,200 kPa in areas away from skid trails. Landings contained greater, but non-significantly different, median compaction values (2,642 ± 325.1 kPa) than skid trails (2,066 ± 229.9 kPa). Compaction levels on landings and skid trails were significantly greater than in areas away from skid trails (1,546 ± 233.8 kPa). Median compaction values were greater for study sites harvested in summer versus winter, but the differences were not significant at $p = 0.05$.

Harvesting Intensity and Regeneration Tree Composition

Overstory residual basal areas ranged from 0 to 26 m^2/ha and were significantly greater in areas away from skid trails (18 ± 1.4 m^2/ha) than on skid trails (13 ± 1.4 m^2/ha) and landings (9 ± 2.0 m^2/ha). Percent cover of tolerant tree regeneration was greater away from skid trails (46 ± 6.4) than on skid trails (45 ± 6.3), and lowest on landings (37 ± 8.9). Percent cover of intolerant tree regeneration was greater on landings (30 ± 3.7) than on skid trails (22 ± 2.6), and away from skid trails (14 ± 2.7).

Interactive Effects of Residual Basal Area and Soil Compaction on Regeneration and Advance Regeneration Tree Species Composition

Higher residual basal area was negatively associated with soil compaction (Figure 3). In general, residual basal area was negatively associated with intolerant regeneration composition, positively associated with tolerant regeneration composition, and varied in the magnitude of its effects with soil compaction. With a full model containing median compaction (COMP), residual basal area (BA) and their interaction (COMP*BA), using a dummy variable for shade tolerance (ST = 0 for shade intolerant and ST = 1 for shade tolerant) on the intercept and all parameters (COMP, BA, and COMP*BA) as independent variables was significant (Table 3). However, with a full model containing COMP, BA, ST, and their interactions (COMP*BA, COMP*ST, BA*ST, and COMP*BA*ST), using a dummy variable for season of harvest (SH = 0 for winter and SH = 1 for summer) on the intercept and all parameters (COMP, BA, ST, COMP*BA, COMP*ST, BA*ST, and COMP*BA*ST) apparently was overspecified and was not significant. Investigating these variables individually or in combination as independent variables indicated that the model with the highest fit, including only significant parameters was equation 1:

[1] Percent regeneration cover = 14.8% + (0.006 kPa)COMP - (0.0002)BA*COMP + (20.8)ST + (1.4)ST*BA - (0.01)ST*COMP

Although results for advance regeneration responses have not been presented thus far, residual basal area negatively correlated with intolerant advance regeneration and positively correlated with tolerant advance regeneration. Soil compaction had no significant correlation with advance regeneration. A full model containing residual basal area (BA), using a dummy variable for shade tolerance (ST = 0 for shade intolerant and ST = 1 for shade tolerant) on the intercept, and BA parameter as independent variables was significant (Table 4). A full model containing BA, ST, and their interaction (BA*ST), using a dummy variable for season of harvest (SH = 0 for winter and SH = 1 for summer) on the intercept and all parameters (BA, ST, and BA*ST) as independent

variables was overspecified and not significant. Investigating these variables individually or in combination as independent variables indicated that the model with the highest fit, was equation 2:

[2] Percent advance regeneration cover = 24.7% - 0.6 m^2/ha (BA) - 9.54(ST) + 2.8 m^2/ha (BA*ST)

Discussion

My results support earlier findings that areas impacted by harvesting machinery will have higher soil compaction levels than areas not trafficked by harvesting machinery (Hatchell et al. 1970, Martin 1988). Even though I do not have exact numbers, it is safe to assume that landings and skid trails received the majority of harvesting traffic, and consequently these areas showed the highest levels of soil compaction (Froehlich et al. 1980, Koger et al. 1984). While winter logging on frozen soil has been found to result in less site disturbance because surface and subsurface effects of soil compaction are minimized (Mace et al. 1971) I could not detect a difference in compaction levels. This may be due to my limited sample size and the degree of variation in other factors. It also may be possible that harvests taking place during winter months did not actually occur on frozen soil, so harvesting machinery may have impacted the site and soil to the same magnitude as on summer harvested sites.

One question from my study arises: do the differences between soil compaction on skid trails versus away from skid trails make a difference in future stand conditions? Stone and Elioff (1998) found significantly greater bulk density values still five years after treatment, and Vora (1988) found greater compaction levels on skid trails 40 years after harvest. Since I am still finding significant differences up to8 years after harvest, I assume that harvesting effects on soil compaction on landings and skid trails could persist throughout most of a rotation. Chapter 2 investigates this issue in greater depth for aspen forests, and can likewise be applied to northern hardwood forests as in this study. Despite the freeze-thaw cycles a northern climate forest endures (Marion 1995), soil

amelioration may not have taken place as of yet, and reasons for that are discussed further in Chapter 2.

I found differences in composition (in terms of proportion of shade tolerant and shade intolerant species) of the tree regeneration between landings, skid trails and areas off the skid trails. This effect has been documented and is usually been attributed mainly to the increased resource availability for seedlings after more intensive harvesting operations. For example, species community structure has been shown to shift along gradients of gap size (McClure and Lee 1993) depending on the disturbance and competitive strategies of pre- and post-harvest vegetation. Phillips and Shure (1990) found tree species richness to increase along a gradient of increasing gap size. Tree species of Minnesota's northern hardwood forest ecosystem display these variations in shade tolerance, and in turn respond differently to gradients of overstory release (Canham 1985, Canham 1989, Kobe et al. 1995, Marks 1975, Runkle 1981, Hibbs 1982, Canham and Marks 1985).

Differences in composition may also be due to different responses to higher soil compaction on skid trails and landings. Reduction in tree growth in compacted areas has been well documented (Chapter two, Bates et al. 1990, Navratil 1991, Schier et al. 1985, Shepperd 1993, Zasada and Tappeiner 1969). These studies and my results indicated that despite differences in species response to residual overstory basal area levels and other site-disturbance related factors, severe soil compaction may be significantly deleterious to tree regeneration.

My results showed that composition of regeneration is related to the interactions of soil compaction and residual basal area. Areas with higher soil compaction and greater overstory removal represented the more disturbed areas of a harvested site. These more disturbed areas therefore encouraged growth of early successional species, which are able to invade disturbed sites and are usually shade intolerant species (e.g., Barnes et al. 1998, Walters and Reich 1996, and Beck and Hooper 1986). Alternatively, especially in stands with advance regeneration, lack of heavy harvesting disturbance encouraged later

successional, shade tolerant species. This phenomenon is also evident in the shift of species composition for the advance regeneration layer along the gradient of harvesting intensity (Béland and Bergeron 1993, Kneeshaw and Bergeron 1996).

The presence of advance regeneration four to eight years after harvest may indicate that it can play an important role in determining future stand composition of northern hardwood forests. In denser stands, shade tolerant species will dominate advance regeneration; and in areas without heavy harvesting disturbance, special management consideration (e.g., felling or herbicide application) may be required to shift the species composition. Alternatively, clearcutting regimes may alter growing conditions too quickly for shade tolerant seedlings. Clearcutting may not provide enough shade and temperature protection which may result in mortality of advance, shade tolerant species, allowing early successional, shade intolerant species to become established (e.g., Bjorkbom and Walters 1986, Walters and Nyland 1989, Greene et al. 1999, Larsen et al. 1997).

Another influence on tree regeneration in northern hardwood stands may be the level of competing herbaceous and other woody vegetation. Highly disturbed areas often provide good habitat for shrubs such as *Rubus* spp. to dominate, often outcompeting regenerating trees and/or preventing seed germination (Yorks and Dabydeen 1999, Smidt and Puettmann 1998). Future investigations are needed to quantify interacting effects of competing vegetation, overstory basal area, soil compaction, and tree species shade tolerance.

Conclusions

This study investigated the effects of harvesting regimes on 15 northern hardwood stands of northern Minnesota, and set out to determine the significant factors affecting tree composition on those study sites. Analyses revealed the significant interaction effects between increased soil compaction, range in residual basal area, tree species shade tolerances, and composition of regeneration and advance regeneration. Management

objectives focused on obtaining "desired" or high quality tree species, must consider their shade tolerance and how they respond to overstory removal and soil compaction. As the level of soil compaction increases, percent cover of tolerant regeneration decreases

Table 1. Study site properties for northern hardwood stands investigated in northeastern Minnesota. Order of northern hardwood sites corresponds to their level of residual overstory basal area. Dominant tree species are given in general for sites with low, intermediate, and high residual overstory basal areas.

Mean Basal Area (m^2/ha) of Residuals	Years Since Harvest	Season of Harvest[a]	Site Index	Dominant Regeneration Tree Species[b]	Dominant Advance Regen Tree Species[b]	Dominant Overstory Tree Species[b]
0	8	W	23	paper birch(29%),	paper birch (29%)	sugar maple (50%)
0	4	W	17	sugar maple (26%)	quaking aspen (29%)	basswood (28%)
3.7	7	S	15		bigtooth aspen (19%)	
4.0	6	W	15			
6.1	4	S	15			
10.9	6	S	17	sugar maple (43%)	sugar maple (30%)	n. red oak (37%)
14.7	5	W	19	ironwood (15%)	n. red oak (23%)	sugar maple (24%)
16.4	6	S	21		red maple (15%)	basswood (14%)
17.5	6	W	20			
18.8	7	W	22			
20.3	4	S	20	sugar maple (70%)	sugar maple (65%)	sugar maple (49%)
21.7	5	W	18		n. red oak (12%)	basswood (20%)
21.7	5	W	22			n. red oak (20%)
23.0	5	W	19			
26.0	8	W	17			

[a] Season of Harvest: W=winter, S=summer
[b] By percent cover

Table 2. Tree species and their shade tolerances. Species investigated on northern hardwood study sites of Minnesota to study regeneration and advance regeneration responses to soil disturbance and residual overstory basal area.

Scientific name[a]	common name	Shade Tolerance[b]
Tilia americana L.	American basswood	tolerant
Ulmus americana L.	American elm	tolerant
Abies balsamea (L.) Mill.	balsam fir	tolerant
Populus balsamifera L.	balsam poplar	intolerant
Populus grandidentata Michx.	bigtooth aspen	intolerant
Fraxinus nigra Marsh.	black ash	intolerant
Prunus serotina Ehrh.	black cherry	intolerant
Picea mariana (Mill.) B.S.P.	black spruce	tolerant
Quercus macrocarpa Michx.	bur oak	tolerant
Juglans cinerea L.	butternut	intolerant
Fraxinus pennsylvanica Marsh.	green ash	tolerant
Ostrya virginiana (Miller) K. Koch.	ironwood	tolerant
Quercus rubra L.	northern red oak	tolerant
Thuja occidentalis L.	northern white cedar	tolerant
Betula papyrifera Marsh.	paper birch	intolerant
Populus tremuloides Michx.	quaking aspen	intolerant
Acer rubrum L.	red maple	tolerant
Pinus resinosa Ait.	red pine	intolerant
Ulmus thomasii Sarg.	rock elm	tolerant
Acer saccharum Marsh.	sugar maple	tolerant
Larix laricina (DuRoi) K. Koch	tamarack	intolerant
Quercus alba L.	white oak	tolerant
Pinus strobus L.	eastern white pine	intolerant
Picea glauca (Möench) Voss	white spruce	tolerant
Betula alleghaniensis Britton	yellow birch	intolerant

[a] based on Gleason and Cronquist (1991) (see further explanation in text)
[b] based on Burns and Honkala (1990)

Table 3. Regression parameters and statistics for describing full and reduced models in the investigation of Hypothesis 3 a: The effects of soil compaction and residual basal area interact with species shade tolerance to significantly influence the percent cover of northern hardwood regeneration.

	Dependent variable: transformed percent cover		
Independent variable	Full Model	Reduced Model	Reduced Model (Eq. 1)
	Regression coefficients (B_i) and statistics		
Intercept	1.06	12.26	14.8
COMP	0.008	0.006	0.006
BA	0.3	0.1	-
ST	35.0	20.2	20.8
SH	28.5	-	-
COMP*BA	-0.0002	-0.0002	-0.0002
COMP*ST	-0.01	-0.008	- 0.01
BA*ST	1.16	1.6	1.4
COMP*SH	-0.007	-	-
BA*SH	-0.4	-	-
ST*SH	-26.1	-	-
COMP*BA*ST	-0.0001	-0.0002	-
COMP*BA*SH	-0.00002	-	-
COMP*ST*SH	0.002	-	-
BA*ST*SH	-0.12	-	-
COMP*BA*ST*SH	0.0002	-	-
R^2 Adjusted	0.295	0.307	0.312
P-value	0.01	<0.0001	<0.0001

Table 4. Regression parameters and statistics for describing full and reduced models in the investigation of Hypothesis 3 b: The effects of residual basal area interact with species shade tolerance to significantly influence the percent cover of northern hardwood advance regeneration.

	Dependent variable: transformed percent cover		
Independent variable	Full Model	Reduced Model	Reduced Model (Eq. 2)
	Regression coefficients (B_i) and statistics		
Intercept	37.0	30.7	24.7
COMP	-0.003	-0.002	-
BA	-0.8	-0.5	-0.6
ST	-8.5	-3.7	9.54
SH	-9.8		-
COMP*BA	-0.0001	-0.0001	-
COMP*ST	-0.001	-0.002	-
BA*ST	2.9	2.4	2.8
COMP*SH	-0.002	-	-
BA*SH	0.8	-	-
ST*SH	16.9	-	-
COMP*BA*ST	-0.0001	0.0002	-
COMP*BA*SH	0.00004	-	-
COMP*ST*SH	-0.005	-	-
BA*ST*SH	-1.5	-	-
COMP*BA*ST*SH	0.0007	-	-
R^2 Adjusted	0.465	0.479	0.476
P-value	<0.0001	<0.0001	<0.0001

Figure 1. Northern hardwood study site locations in Minnesota.

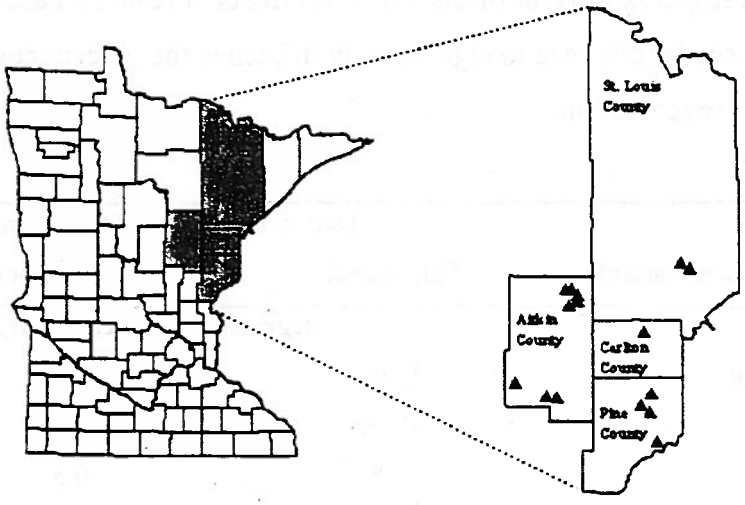


Figure 2. Field collection methods to investigate tree species composition according to percent cover. Relevé plots were placed within each study site. One "L" plot was placed in or adjacent to the landing, two "S" plots were placed within skid trails, and two "A" plots were placed away from skid trails and landings. Data were collected to quantify regeneration, advance regeneration, residual basal area, and soil compaction.

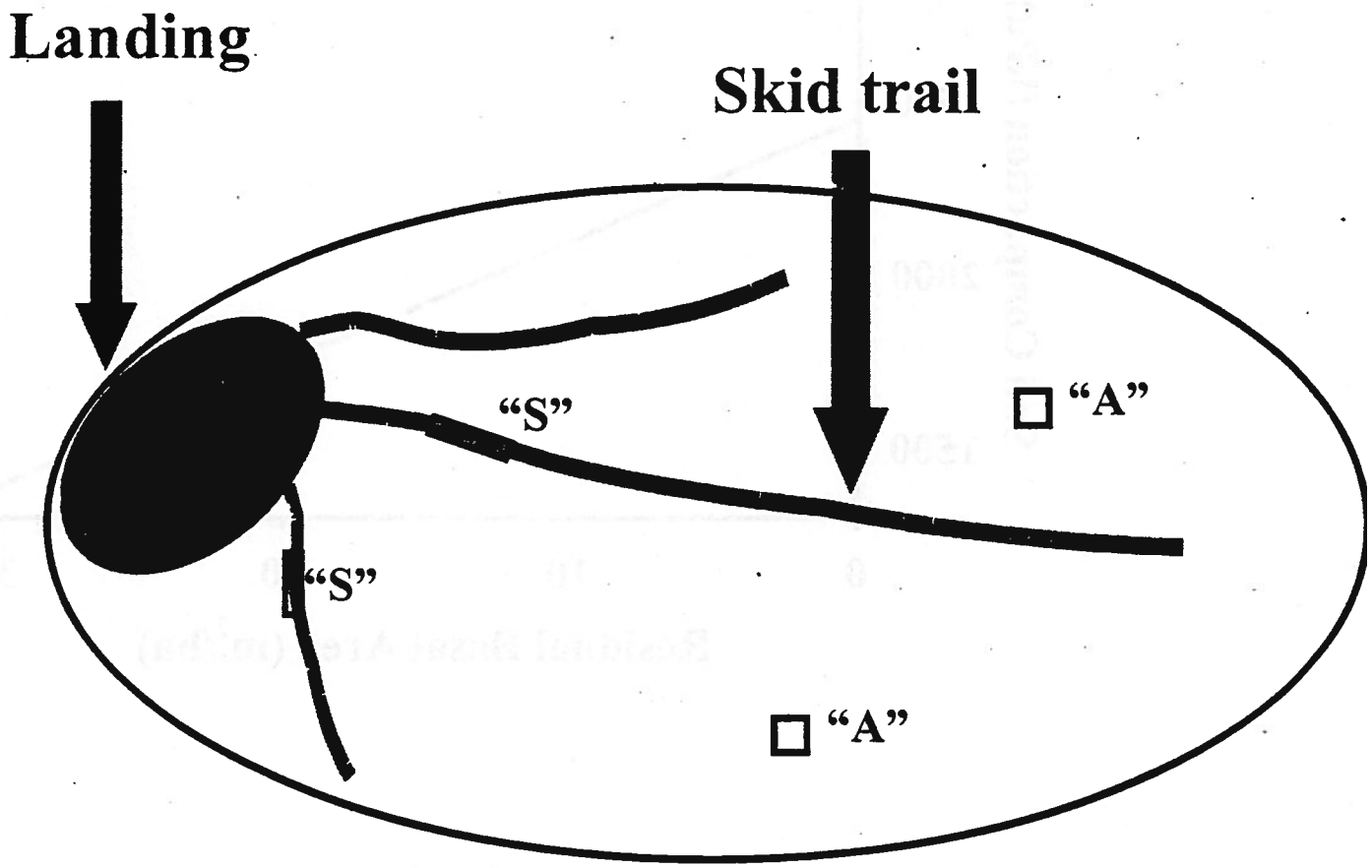
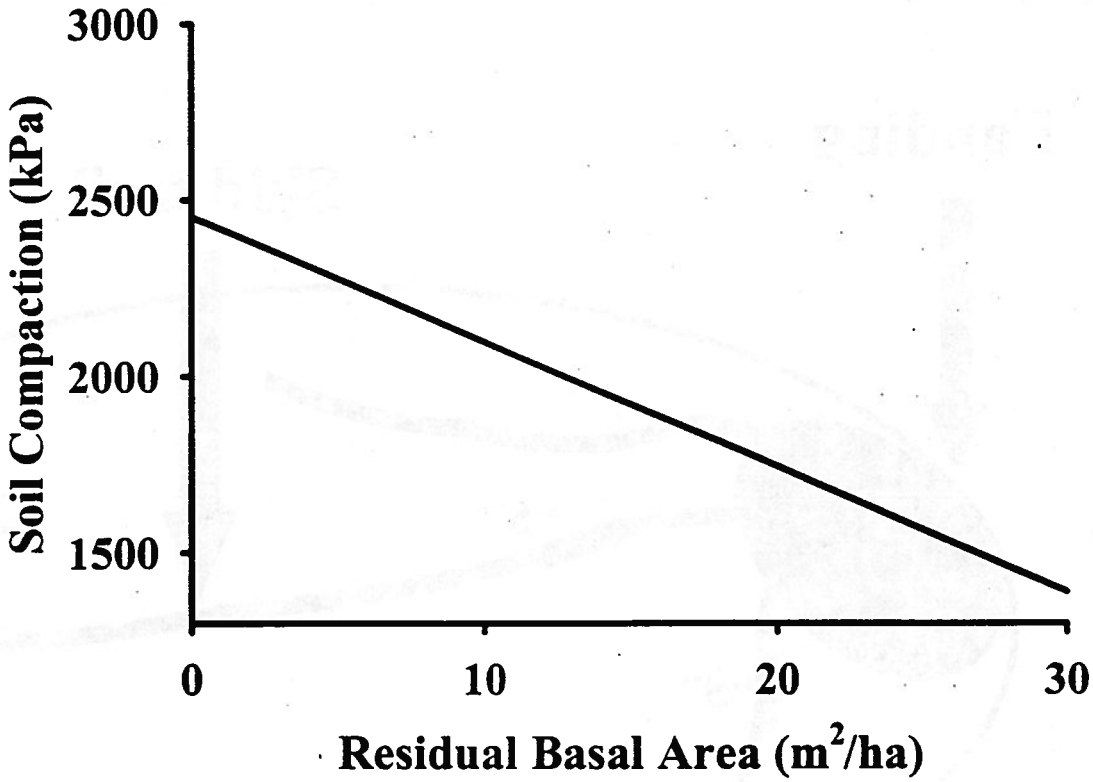


Figure 3. Residual basal area (m^2/ha) versus soil compaction (kPa). Sites investigated were hardwood partial harvests and clearcuts in northeastern Minnesota.



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HARVESTING IMPACTS ON SPECIES DIVERSITY AND COMPOSITION IN NORTHERN ASPEN FORESTS: THE INFLUENCE OF HARVEST SEASON AND WITHIN-SITE DISTURBANCE PATTERNS

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Background

The trembling aspen ecosystem covers around 5 million acres in Minnesota (Jaakko Pöyry Consulting Inc. 1992) and is an important source for fiber and high quality sawtimber. The Generic Environmental Impact Statement study predicted intensive management of this covertype in the future (Jaakko Pöyry Consulting Inc. 1992). A better understanding of impacts from such intensive management is necessary as greater emphasis is being placed on balancing multiple uses of the forest *e.g.* recreation, timber production and maintenance of biodiversity (Franklin et al. 1989, Edwards and Abivardi 1998).

Impacts of harvesting on sustainability of forests can be described by the stability (i.e. resistance to change) and the resiliency (i.e. rate at which a community returns to its initial state) (Halpern 1988). It has been difficult to generalize the relationship between biodiversity and ecosystem processes such as productivity (Cardinale et al. 2000) but it is generally accepted that increased biodiversity in a system provides a buffer against fluctuations in the environment, which may be important in the maintenance of long term stability of the ecosystem processes (Loreau 2000, Schwartz et al. 2000).

Disturbance as a primary factor influencing diversity and floristic composition in forested systems has been under great scrutiny (Grace 1999, Roberts and Gilliam 1995). In general terms, disturbance through modification of environmental factors such as heat, moisture and wind together with the availability of propagules, harvesting impacts to soils, and animal life, determine the response of the vegetation to the harvesting activities. Various approaches are useful in describing the patterns of

vegetation in response to disturbance; most commonly using the regeneration niche (Grubb 1977) in combination with the colonization strategies and life history attributes for the component species (Bazzaz 1996, Grime 1979). For example, aspen has a specific regeneration niche, which consists of a lack of dominant shoot (e.g., removed by harvesting operation), high light conditions, and warm soils, and in combination with its colonization strategy of root suckering, aspen can be viewed as a pioneering species. The composite flora in an aspen dominated ecosystem contains a complex arrangement of pioneering, generalist and interior forest species, each using a combination of strategies. Interior forest species more sensitive to disturbance generally rely heavily on vegetative reproduction through rhizomes or vegetative propagules (Lezberg et al. 1999), while generalists can rely on a combination of root, seedlings and seed and or bud banks (Haeussler et al. 1990). Competitive relationships between interior forest herbs, shrubs and more ruderal species can be very site specific and dependent upon the temporal and spatial patterns created within each site (Collins et al. 1985). Whether or not the presence of a species remains constant, increases or decreases in response to disturbance depends not only on the strategies mentioned above but on the interaction of these strategies with the intensity and duration of the disturbance (Denslow 1985, Grace 1999).

Trembling aspen (*Populus tremuloides* Michx.) is a shade intolerant species (Baker 1949) and naturally regenerates through suckering after large scale disturbances that remove most or all of the overstory (Perala 1990). It is most commonly harvested by clearcutting because this method improves regeneration conditions for aspen by complete removal of the overstory (Perala 1977, Schier et al. 1985). Disturbances, such as clearcutting, usually assure that aspen regenerates, but may not act at an appropriate scale (temporally or spatially) to allow for the persistence or stability of associated understory species (Connell and Sousa 1983). The intensity of harvesting varies by site and the associated conditions thus creating variability in the disturbance gradient. For example, the effects of harvesting on soil properties and regeneration differ by season of the year (Bates 1990, Smidt 1996). Winter harvesting generally has less impact on soil properties than summer harvesting. With a deep snow pack and frozen soil, the forest floor and surface soil change little during harvesting. Snow properties may change during harvest and this may help to protect the soil (Zasada et al. 1987). However, winter logging can result in damage to soils if the snow depth is not adequate and/or soils do not freeze. A particularly sensitive time is late winter when the snow is melting and surface soil becomes saturated with water. Many studies have investigated the effects of logging on soil disturbance during the snow-free period. Three types of disturbances associated with harvesting are soil compaction, rutting, and scarification (Bates 1990). Soil compaction has been shown to limit root growth of a variety of tree species (Ruark et al. 1982) and reduced the amount and growth of quaking aspen suckers (Alban et al. 1994). Several authors note the

absence or lower density of aspen suckers on skid trails and landings (Zasada and Tappeiner 1969, Schier et al. 1985, Shepperd 1993, Bates 1990). Logging disturbance and compaction also affect overall plant species composition. For example, exotic plants can invade on skid trails and compacted areas affecting regeneration and growth of tree regeneration and other native plants (Alban et al. 1994). Ruts or depressions are created when tires break through the forest floor into the mineral soil. Rutting can lead to direct injuries to root systems (Shepperd, 1993). Scarification is the exposure of mineral soil by displacing the organic matter. Large-scale scarification can result in lower site quality and reduced future productivity (Tuttle et al. 1985). High intensity mechanical site preparation such as trenching and plowing resulted in an increased abundance of non-native species within a sub-boreal coniferous forest of central British Columbia (Haeussler et al. 1999). Small scale scarification and mixing of organic matter often improve regeneration conditions by improving seedbed conditions for a variety of species.

Our study is a retrospective exploration of harvesting impacts on understory vegetation *i.e.*, the gradient of disturbance as represented by soil compaction and overstory removal within the aspen covertype in northern Minnesota. Specifically we characterize the disturbance gradient of different treatments by considering the timing of harvest, soil properties, and overstory composition.

Our objective was to test following hypotheses:

1) Whether compaction levels on aspen sites differ between areas with high, intermediate and low disturbance and vary with season of harvest (summer vs. winter).

2) Whether understory species composition will be influenced by the harvesting impact or level of disturbance (*i.e.*, landings, skid trails, and off skid trails) and whether this influence differs between sites harvested in summer vs. winter.

Methods

Study sites

Sites used in this study were selected from the quaking aspen covertype. Major species of the aspen covertype in Minnesota are quaking aspen (*Populus tremuloides* Michx.), bigtooth aspen (*Populus grandidentata* Michx.) and balsam poplar (*Populus balsamifera* L.). Associated species of the aspen covertype include balsam fir (*Abies balsamea* (L.) Mill.), black spruce (*Picea mariana* (Miller) BSP.), paper birch (*Betula papyrifera* Marsh.), sugar and red maple (*Acer saccharum* Marsh., *A. rubrum* L.), northern red oak (*Quercus rubra* L.) and basswood (*Tilia americana* L.). Less common associates

include American elm (*Ulmus americana* L.), and black and green ash (*Fraxinus nigra* Marsh. and *F. pensylvanica* Marsh.). The region has a temperate climate with mean monthly temperatures ranging from -18 to 17° C and a mean annual temperature of 1.6° C. Average annual snowfall is about 380 cm. Average seasonal precipitation ranges from 144 mm in winter to 122 mm in the summer. Soils for this region are derived from till plains, outwash and moraines laid down by glacial advances (Anderson et al. 1996).

A total of 19 sites, that were clearcut between 1988 and 1994, were selected from timber sales in 6 counties northeastern Minnesota, resulting in an average age of 6 years for the study period. Average residual basal area remaining ranged from ≤ 1 m^2/ha to 9 ± 6.5 m^2/ha (4 to 39 ft^2/acre). Detailed information regarding the site conditions (broken down by disturbance categories) are presented in Table 1. Sites were chosen to avoid other types of disturbance due to human activity as well as natural disturbances such as windthrow or insect outbreak. Study sites ranged in size from 3 to 14 ha ($\bar{x} = 9$ ha or 25 acres) with an average aspen 50-year site index of 24 m (78 feet). Sale documentation and personal communication with sale administrators allowed us to split sites into groups based on season of harvest (summer vs and winter). However, it was not possible to reconstruct whether soils were actually frozen on sites harvested in winter.

Sample design

Plot layout was designed to cover the gradient of disturbance conditions created through harvesting within each site. First, harvesting patterns, i.e., network of skid trails and landings were identified and areas were labeled based on the amount of harvesting traffic they received (e.g., Figure 1). Landings (L) receive the highest amount of traffic and thus experience the maximum harvesting disturbance on a site. Skidtrails (S) receive less traffic and thus less harvesting disturbance. Areas off the landings and skid trails (O) had little to no harvesting traffic and were viewed as "controls". Vegetation plots (60 m^2) were then placed randomly on areas in each of these categories (1 plot in L, 2 plots in S, 2 plots in O). On each vegetation plot, the relevé method (Mueller-Dombois and Ellenberg 1974) was used to inventory all vascular plant species for the 0-2.0 m height stratum. Inventory was conducted during June through August in 1997 and 1998. Vascular plant species occurrences were recorded and each species placed in a cover class: (1) single occurrence, (2) <5% (occasional), (3) <5% (plentiful), (4) 5-25%, (5) 26-50%, (6) 51-75%, and (7) 76-100%. Median percent values were used to represent each cover class in the analysis. Nomenclature for all vascular plants follows Gleason and Cronquist (1991).

Measurements of tree regeneration and residual basal area (m^2/ha) were taken on a one 0.001 ha regeneration-overstory plot (2-m x 5-m) placed in the center of each vegetation plot (Figure 1). Diameters (mm) of all tree species > 2.54 cm diameter at breast height (DBH) were measured with a caliper or diameter tape. Residual trees were defined as those trees left standing during harvest with a minimum DBH of 18 cm. Basal area for residual trees was measured from the center of each regeneration plot using a 1-meter factor prism.

Soil compaction was characterized by measuring the resistance to penetration (kPa) of the soil matrix using a soil cone penetrometer (Bennie and Burger 1988). A minimum of ten measurements were taken to characterize compaction in the top 15 cm of the soil horizon in each vegetation plot and these data were used to calculate median soil compaction value. Soil texture to 50 cm was determined from five soil samples collected on each site using an adapted hydrometer method (Grigal 1973).

Data Treatment

Absolute soil compaction data were quite variable, likely due to the inherent differences in soil texture, soil moisture and topography between sites. To account for inherent site differences, median compaction values were standardized for each site. Soil compaction and regeneration density values for all plots were divided by the respective values found in the "O" plot with the lowest compaction value and thus "standardized" compaction and density values were calculated.

Floristic diversity was characterized by species richness (S), i.e., number of species/plot and evenness (J) (Pielou, 1975). To calculate J, first the Shannon's index of diversity (H') was calculated, using:

$$H' = -\Sigma(p_i \ln(p_i))$$

where p_i is the proportion of the ith species in the plot (Margurran 1988). Second J itself was calculated using:

$$J = H'/\ln(S).$$

For the ordination and classification analysis the influence of transient species within the analysis was reduced by trimming species that occurred on < 3% of all the 95 vegetation plots (Legendre and Legendre 1998).

Analysis

PCORD 3.05 (McCune and Mefford 1997) was used for ordination and classification analysis. Outlier analysis was conducted within PCORD using a cutoff of 2 standard deviations of the Euclidean Distance as well as by inspection of graphical placement of plots along ordination axes. JMP 3.1 (SAS Institute 1999) was used to perform Analysis of Variance Analysis (ANOVA). Histograms of data within disturbance categories were examined for evidence of outliers. If ANOVA results were significant, the Tukey-Kramer HSD multiple comparison of means procedure (Kramer 1956) which preserves an experiment-wise error rate of 0.05 was employed. A modified LSD test (Welch 1951) was applied when variances within groups were unequal. Throughout the analysis, the terms significant and highly significant refer to $\alpha \leq 0.05$ and $\alpha \leq 0.01$, respectively.

Soil disturbance – ANOVA and Tukey-Kramer (HSD) procedures were used to test whether areas in landings (L), skid-trails (S) and areas off skid-trail and landings (O) varied in their compaction values, and whether compaction values differed between summer and winter harvested sites.

Floristic composition - Detrended Correspondence Analysis (DCA) (Hill and Gauch 1980, Ter Braak. 1995) was used to test whether grouping of plots based on understory species composition is influenced by disturbance (L, S, and O) and season of harvest (summer and winter). DCA ordination diagrams were used to judge the placement of plots along axes based on their similarity in species composition. To avoid disproportionate influence of the aspen regeneration, all species of aspen were removed from the species by plot matrix. Interpretation of variation along DCA axes was aided by constructing a second matrix with categorical variables: disturbance level (L, S, and O), and season of harvest (summer and winter).

A nonparametric classification procedure was used to test the significance of species composition within the disturbance level by season of harvest matrix. The procedure relates the plots within categorical groups to a random allocation of plots using Multi-Response Permutation Procedure (MRPP) developed by Mielke (1984). In this method, the actual within group compositional similarities (δ, i.e., within group Euclidean distance) and expected compositional similarities ($\bar{\delta}$ for all possible groupings of the plots) are compared. The test statistic (T) is then calculated as $T = (\delta - \bar{\delta}) / \mu_\delta$ where μ_δ is the standard deviation of δ under the null hypothesis (Zimmerman et al. 1985). For categorical groups determined to be significant in uniquely identifying species assemblages, Indicator Species Analysis was used to identify specific species characteristic of those groups. For this, an indicator index value (IV) is

assigned to a species based on a combination of the species relative abundance and relative frequency values. For example, the maximum IV of 100 is assigned to a species with perfect indication for a group, i.e., when all individuals of a species occur in a single group and when the species is present in every site within that group. The actual IVs are a percent of perfect indication for a group. The null hypothesis that species had no indicator value was tested using a Monte Carlo permutation technique using 1000 permutations (for more detail see Dufrene and Legendre 1997).

ANOVA and Tukey-Kramer (HSD) tests were conducted for understory species richness (S) and understory evenness (*J*) by disturbance level and season of harvest.

Other Factors – To investigate potential confounding factors on understory composition, ANOVA was used to compare difference between sites harvested in summer vs. winter for the following independent site variables: 1) the influence of competition from tree regeneration (standardized tpha), 2) from residual overstory (BA) and 3) soil texture (% sand).

Results

Soil compaction

Disturbance gradient – For summer and winter plots, mean levels of soil compaction (standardized) in landings and on skid trails (L and S) were essentially the same (Table 2a.). While mean levels of soil compaction for L and S plots for summer harvested sites were both significantly greater than mean standardized compaction on plots in the O disturbance category, in winter harvested sites, only the mean level of soil compaction on S plots was significantly greater than that of the O plots (Table 2a).

Season – Because of the results testing the difference between disturbance categories (Table 2a), L and S categories were combined for testing the influence of season of harvest on soil compaction. Comparison of means for the L and S categories showed a significantly higher compaction levels on summer harvested sites (Table 2b). There was no significant difference in compaction levels between summer vs winter sites for the O category (Table 2b).

Floristic composition

Disturbance – Disturbance categories were useful in identifying the major gradients in DCA for both summer and winter harvested vegetation plots. Specifically, DCA revealed that within summer sites Axis I and II explained 22% of the variation and represented the major compositional gradients. Axis II scores

seemed most related to the disturbance categories with higher scores for most of the O vegetation plots. L and S vegetation plots greatly overlap in ordination space, with lower DCA scores for Axis II revealing their similarity in plant composition. O vegetation plots appear as a distinct cloud of points only slightly overlapping the L and S vegetation plots. MRPP showed that species composition in L and S vegetation plots was not significantly different ($T = 0.34$, $P = 0.28$). On the other hand, vegetation in O plots was distinctly different from the "higher disturbance" plots, i.e., L and S plots combined ($T = -4.31$, $P < 0.004$). Similarly, DCA of winter vegetation plots revealed that Axis I and II were the major gradients, explaining 30% of the variation. Axis I scores were most related to the disturbance categories with higher scores for the L and S vegetation plots. Although in ordination space L and S vegetation plots overlap while O plots remain more distinct, MRPP was able to distinguish L vegetation from S vegetation as well as each of these from O vegetation, with each disturbance category significantly unique in vegetative composition (L vs. S, $T = -1.91$, $P = 0.05$; S vs O, $T = -6.77$, $P < 0.001$; L vs O, $T = -4.29$, $P = 0.001$).

Season - DCA of vegetation data from all disturbance categories combined did not show distinctly separate groups by season of harvest. Since the O category of vegetation plots had lower levels of compaction and distinctly different vegetation composition, inclusion of these plots potentially disguised the influence season of harvest had on species composition. In light of this, O vegetation plots were removed to conduct a revised ordination. The revised ordination revealed that Axis I and II explained 37 % of the variation (Fig. 2a). Summer harvested plots, while overlapping somewhat with winter harvested plots, were more tightly clustered into a distinct cloud ($\delta = 60.7$) than the winter harvested plots ($\delta = 66.1$; Fig. 2a). The distinctness of species composition by season of harvest was confirmed for L and S plots combined using MRPP ($T = -4.13$, $P = 0.005$). In order to assess whether this difference may be due to inherent site difference between summer and winter harvested sites, rather than a result of harvesting disturbance, an ordination of only O vegetation plots was conducted. As shown in Figure 2b, summer and winter O vegetation plots overlap along both Axis I and Axis II and reflect less coherent groups by season of harvest. While plots appeared to group slightly in ordination space, MRPP did not detect a difference in species composition by season ($T = -0.59$, $P = 0.24$). Also, differences in variability of species composition by season, was less distinct ($\delta = 68.7$ and $\delta = 72.5$ for summer and winter, respectively).

Species Groups - Indicative species for both summer and winter sites were identified by combining L and S plots vs. O plots, resulting in two main disturbance groups (high and low). Species that were found to be significant for identifying high vs. low disturbance groups overlapped by season of harvest (Tables 3a and 3b). Both winter and summer harvested sites revealed a compositional shift (dominance) of species

due to changes in relative frequency or relative abundance within the site or both in combination. For example, in both summer and winter sites, higher disturbance plots contained grass and invasive forb species that were not present on low disturbance plots (e.g., zero relative frequency and relative abundance for low plots, Tables 3a and 3b). Two of these species were naturalized European grasses often used in pastured systems. Interior forest species tended to decrease in dominance (e.g., *Maianthemum canadense* Desf., and *Clintonia borealis* (Aiton) Raf.), with lower relative frequency of occurrence and lower relative abundance on higher disturbance plots than on low disturbance plots). An interior forest species considered to be generalist, *Aster macrophyllus* L. while maintaining similar relative frequencies between higher and lower disturbance plots, had a lower relative abundance on higher disturbance plots (Table 3b). In comparison, a generalist shrub such as *Rubus idaeus* L. also maintained similar relative frequencies between disturbance groups but as expected of an increaser, relative abundance was greater on higher disturbance plots (Table 3a and 3b). Overall the pattern of greater dominance by increaser and invasive type species on higher disturbance plots was similar between winter and summer harvested sites. There was some indication that winter harvested sites were more inherently mesic in species composition, with species suited to moist conditions present on both high and low disturbance plots (*e.g Scirpus cyperinus* (L.) Kunth., *Salix spp.* L., in high disturbance plots and *Botrychium virginianum* L. (Swartz), *Ulmus Americana* L. in lower disturbance plots).

Species Richness and Evenness – On summer and on winter harvested sites mean species richness was not significantly different for vegetation plots between L and S disturbance categories (Table 4a.). While both L and S plots had significantly greater mean richness than O plots in summer harvested sites, in winter harvested sites only mean richness of S plots was significantly greater than O plots (Table 4a.). Mean evenness of species for plots on both summer and winter harvested sites was not significantly different for any category of disturbance ($F_2 = 0.27$, $P = 0.766$; $F_2 = 1.39$, $P = 0.26$ for summer and winter, respectively). To assess the impact of inherent site differences between summer and winter sites, *i.e.*, using only O vegetation plots, mean richness was significantly higher for winter harvested sites ($F_1 = 10.19$, $P = 0.003$) while mean evenness was not significantly different by season of harvest ($F_1 = 0.80$, $P = 0.38$). On the other hand, both mean richness and evenness on the higher disturbance (L and S) vegetation plots combined were significantly lower on summer-harvested sites (Table 4b).

Other Site Influences – While aspen species were excluded from the ordination matrices, effects of competition from aspen regeneration on understory plant composition were judged by their influence on low disturbance (O) plots in summer vs. winter harvested sites. O plots were chosen because they contained the highest aspen regeneration density for both summer and winter harvested sites (Table 5).

Aspen regeneration density on O plots was not significantly different by season of harvest ($F_2 = 0.81$, $P = 0.38$). At the same time mean richness was higher on winter harvested O plots, indicating that competition from aspen regeneration was not responsible for lowering diversity on summer harvested sites. Residual overstory density for both summer and winter harvested sites did not differ between disturbance categories ($F_2 = 0.17$, $P = 0.85$; $F_2 = 0.06$, $P = 0.94$, for summer and winter, respectively). Soil texture (% sand) was significantly greater for summerharvested sites ($F_2 = 17.60$, $P < 0.0001$).

Discussion

Our results are confined to the "initial effects" (sensu Halpern and Spies 1995) of harvesting disturbance such as soil compaction and removal of overstory but indicate that these initial effects through extent and timing of harvest influence not only the richness but also the composition of the vegetation. Mechanisms for shifts in diversity and composition of vegetation due to disturbance can be viewed within the context of intermediate disturbance hypothesis (Connell 1978) in addition to that of successional stand dynamics (Oliver and Larson 1990). Our results indicate that disturbance patterns created within site through clearcut harvesting were heterogeneous and even though clearcuts are considered to be one of the more homogeneous disturbances on the landscape, a range of disturbance and thus diversity conditions were created. For example, off trail (O) plots represent an intermediate level of disturbance within the site i.e., removal of overstory which stimulated regeneration plus limited soil disturbance while the landing (L) and skid trail (S) plots had the least amount of regeneration and the highest soil disturbance. Diversity and composition within sites were reflected as a range of neighborhoods with different within neighborhood diversity patterns. While similar patterns due to disturbance occurred on both summer and winter harvest, more heterogeneous species composition existed on winter sites. These results support De Grandpré and Bergeron (1997), who found less change in plant composition in more diverse environments, but in this case our results are confounded by the season of harvest, i.e., more diverse sites had less disturbance. In other words, it is likely the combination of less initial diversity coupled with higher impact through soil compaction that led to greater changes in the plant community on summer harvested sites. Results of a study of varying intensities of silvicultural site preparation treatments in a boreal mixed forest, found that the diversity of understory vegetation increased as compared to undisturbed treatments but did not vary according to intensity of disturbance while species composition did vary with intensity of disturbance (Peltzer et al. 2000). Similar to Peltzer et al. (2000), Haeussler et al. (1999), also looking at intensities of site preparation on vegetation, found that severity of disturbance influenced species composition but in contrast influence on diversity of

species varied across sites within the study. In general compositional differences were due to higher abundance of non-native species occupying the most intensely disturbed areas (Haeussler et al. 1999).

The plant communities of aspen forests have very little time to recover when considering the fairly short rotation time of 45-50 years. This can be important from the standpoint of the maintenance of rare or native plant populations. Initial and remnant understory vegetation of harvested sites are linked to the rate of recovery (Rydgren et al. 1998), with higher proportions of ruderal species extending the recovery time as well as altering the trajectory of the site (Halpern 1988). In our study, the patches with least disturbance may act as species pools (Zobel 1997) that over time, as the canopy closes, provide a source of interior forest species to re-colonize the site. Interior forest herbs use a variety of below ground strategies that enable them to persist in disturbed sites (Lezberg et al. 1999). Although these interior forest species may be available to colonize the more disturbed patches, they are often less competitive than ruderal species in more harsh microclimates (Meier et al. 1995). Again, competition with more ruderal species could slow the rate of recovery or even alter the long term composition of the site by encouraging a greater amount of ruderal species in the soil seed bank (*e.g.* on our study sites *Rubus ideas* L.,). One study of understory vegetation response to clearcutting found that competition with blackberry (*Rubus allegheniensis* T.C. Porter) was likely more influential on diversity than that of regenerating tree species (Yorks and Dabydeen 1999). On sites with greater areas in skid trails and landings, persistence may not be enough, for example a study looking the reproductive ability of herbs, found evidence that there was a threshold size required for sexual reproduction to occur and that there were differences in reproductive ability of plants derived from seeds and those derived from rhizomes, the later allocated more energy to sexual reproduction and clonal growth (Schmid et al. 1995). Additionally, the proximity of intact lower disturbance patches is likely to be important in re-colonization. Spatial distribution of remnant forest species was strongly related to the location of new plants after disturbance created through canopy removal in a northern hardwood forest (Hughes and Fahey 1991). All of these factors point to the importance of limiting not only thelevel of disturbance but also the area impacted, thus maintaining a spatially connected network of remnant forest patches that are large enough to contain reproductively viable interior forest species.

Management implications

Harvesting, even clearcutting, is a complex disturbance and generalization about the response of understory vegetation to clearcutting have to be made very carefully. Clearcutting leads to a complex matrix of disturbance intensities, e.g., landings and skidtrails are highly disturbed and consequently

understory vegetation on these areas shifts toward invasive, pioneer species, typically grasses and sedges. On the other hand, areas not in skidtrails and landings (the majority of the site) are less impacted and maintain a more stable vegetation community. In the long term, as stands develop, this may allow for reintroduction of species on skidtrails and landings, that were displaced during harvesting. On the other hand, landings and skid trails may facilitate establishment of invasive species that potentially may invade undisturbed portions of the sites later. The sites selected for winter harvest - mainly due to soil moisture conditions - have intrinsically higher understory vegetation diversity. In addition, the disturbance due to harvesting, as measured by soil compaction, is less on winter harvested sites. Together this results in a more stable vegetation community on winter harvested sites. These finding stress the importance of designing harvests to minimize the area in skid trails and landings not only to maintain aspen productivity (see Arikian 2001), but also for maintaining understory vegetation diversity.

The question remains how quickly these ecosystems recover, i.e., how multiple entries impact understory vegetation. In a related study, we were unable to determine the location of skid trails 30 to 50 years after harvest (Berger and Puettmann 2000, data not shown). Our study suggests that mapping designated skid trail systems and utilizing the system for future entries may be especially important on summer harvested sites.

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Table 1. Site descriptions by season of harvest: Site code, Age (growing seasons since harvest), SI - aspen 50-y site index. Mean compaction, aspen regeneration and residual basal area are given by disturbance categories Landing (L, n=1), Skid-trail (S, n=2) and controls (Off landings and skid-trails) (O, n=2). Values in parenthesis represent ± 1SE.

			Compaction (kPa)			Aspen Regeneration (tpha)			Residual BA (m^2/ha)		
	Age (y)	SI (m)	L	S	O	L	S	O	L	S	O
Summer (n=45)	7	24	5599	7398 (1131)	5524 (3499)	0	2500 (3536)	42500 (14849)	0	0	0.5 (0.7)
	7	23	4399	4249 (1901)	1400 (71)	0	500 (707)	11000 (4243)	0	1.5 (2.1)	0
	6	24	1200	1475 (177)	1200 (0)	0	500 (707)	5500 (2121)	4	7.5 (0.7)	12.5 (10.6)
	6	24	1550	1975 (601)	1125 (106)	0	17000 (24042)	37500 (50205)	8	0	0
	5	22	4199	4999 (0)	3799 (707)	0	5000 (7071)	22500 (17678)	0	7.5 (2.1)	13 (5.7)
	5	26	6098	5899 (1979)	4150 (2333)	0	17500 (24749)	29500 (12021)	0	0	0
	6	24	2499	2000 (141)	1350 (495)	0	0	2500 (3536)	4	2.5 (0.7)	3 (2.8)
	4	20	6398	3099 (706)	3299 (1273)	0	5000 (0)	54500 (2121)	0	1 (1.4)	0
	5	21	7648	7898 (141)	3999 (141)	21000	500 (707)	38000 (24042)	2	0.5 (0.7)	3 (2.8)
Winter (n=49)	6	23	7198	3249 (2474)	6398 (566)	0	5000 (7071)	35500 (7779)	0	0.5 (0.7)	0
	5	23	1600	1650 (212)	2699 (707)	7000	17000 (2828)	44000 (2828)	2	0	0
	4	23	4599	6698 (141)	2974 (672)	10000	10000 (4950)	37500 (12021)	0	3.5 (2.1)	0
	6	23	6198	6148 (2757)	4849 (495)	0	9000 (0)	19500 (12021)	0	0	1 (1.4)
	6	25	7998	6948 (71)	4249 (495)	0	3500 (0)	47000 (9900)	1	1 (0)	2 (2.8)
	11	15	5399	4699 (1838)	3699 (283)	0	0	29000 (11314)	0	0	1 (1.4)
	4	23	3399	5949 (707)	2100 (--)	10000	0	41000 (--)	5	0.5 (--)	1 (--)
	11	23	4599	5949 (71)	4049 (2333)	0	0	20500 (4950)	0	0	0
	8	24	3199	6248 (212)	4399 (2823)	3000	9500 (3536)	11000 (1414)	0	0	0
	6	24	6698	4249 (636)	6498 (1273)	10000	500 (707)	16500 (6364)	0	0.5 (0.7)	2 (1.4)

* missing one O plot

Table 2a. ANOVA and TKHSD means comparisons for compaction in disturbance categories Landing (L), Skid-trail (S) and Off (O) grouped by season of harvest (summer vs. winter). Different lower-case letters indicate significantly different ($p = 0.05$) means for disturbance categories.

Disturbance	Mean ± SE Summer	n	Mean ± SE Winter	n
L	214.38 ± 23.54 a	8	156.44 ± 19.61 ab	9
S	204.5 ± 16.65 a	16	164.72 ± 13.86 a	18
O	129.06 ± 16.65 b	16	110.81 ± 14.70 b	16
	$F = 6.77$, df = 2		$F = 9.35$, df=2	
	$p = 0.003$		$p = 0.002$	

Table 2b. ANOVA and TKHSD means comparisons for compaction by season of harvest with plots combined for disturbance categories (L and S, O). Different lower-case letters indicate significantly different ($p = 0.05$) means for season categories.

Season	Mean ± SE L and S plots	n	Mean ± SE O plots	n
Summer	207.79 ± 14.84 a	24	129.06 ± 9.62 a	16
Winter	161.96 ± 13.99 b	27	110.81 ± 9.62a	16
	$F = 5.05$		$F = 1.80$	
	$p = 0.029$, df = 1		$p = 0.20$, df = 1	

Table 3a. Species indicative of disturbance categories within summer harvested sites. The Maximum IV was used to test significance for species by disturbance category ($p \leq 0.05$). Relative abundance and relative frequency show the shift in dominance of species by disturbance groups.

		Relative Abundance (%)		Relative Frequency (%)		
	Species	**High plots**	**Low Plots**	**High Plots**	**Low Plots**	**Max IV**
High	*Agrostis gigantea* Roth	100	0	29	0	29
	Betula papyrifera Marshall	77	23	92	56	70
	Erigeron strigosus Muhl.	100	0	33	0	33
	Fragaria virginiana Duchesne	77	23	88	81	68
	Geum aleppicum Jacq.	100	0	33	0	33
	Juncus tenuis Willd.	100	0	33	0	33
	Phleum pratense L.	100	0	33	0	33
	Poa spp. L.	100	0	33	0	33
	Rubus ideaus L.	71	29	96	81	68
	Taraxacum officianale Weber ex Wiggers	84	16	88	19	74
Low	*Abies balsamea* (L.) Miller	30	70	33	63	44
	Acer rubrum L.	32	68	50	81	55
	Acer saccharum L.	11	89	33	63	56
	Acer spicatum Lam.	14	86	33	56	48
	Anemone quinqefolia L.	18	82	17	50	41
	Apocynum androsaemefolium L.	28	72	29	56	40
	Aralia nudicaulis L.	16	84	46	94	80
	Clintonia borealis (Aiton) Raf.	18	82	29	69	57
	Corylus cornuta Marshall	20	80	71	94	75
	Impatiens capensis Meerb.	0	100	0	19	19
	Lonicera canadensis Marshall	20	80	21	56	45
	Maianthemum canadense Desf.	26	74	50	88	65
	Rubus pubescens Michx.	33	67	25	69	46
	Streptopus roseus Michx.	25	75	33	63	47

Table 3b. Species indicative of disturbance categories within winter harvested sites. The Maximum IV is used to test significance for disturbance category ($p \leq 0.05$). Relative abundance and relative frequency show shift in dominance of species by disturbance groups.

		Relative Abundance (%)		Relative Frequency (%)		
	Species	**High plots**	**Low Plots**	**High Plots**	**Low Plots**	**Max IV**
High						
	Achilliea millefolium L.	100	0	26	0	26
	Agrostis gigantea Roth	100	0	30	0	30
	Betula papyrifera Marshall	77	23	78	19	60
	Carex spp L.. (Ovales type)	90	10	48	6	43
	Fragaria virginiana Duchesne	80	20	96	88	77
	Juncus tenuis Willd.	100	0	30	0	30
	Onoclea sensibilis L.	100	0	22	0	22
	Phleum pratense L.	100	0	33	0	33
	Poa spp. L.	100	0	33	0	33
	Prunella vulgaris L.	100	0	30	0	30
	Rubus ideaus L.	76	24	96	88	73
	Salix spp L.	98	2	56	6	55
	Scirpus cyperinus (L.) Kunth.	100	0	44	0	44
	Taraxacum officianale Weber ex Wiggers	82	18	63	13	52
	Trifolium hybridum L.	100	0	37	0	37
Low	*Anemone quinqefolia* L.	25	75	26	75	56
	Aralia nudicaulis L.	19	81	59	100	81
	Aster macrophyllus L.	21	79	93	100	79
	Botrychium virginianum L. (Swartz)	15	85	4	25	21
	Carex pensylvanica Lam.	7	93	11	44	41
	Clintonia borealis (Aiton) Raf.	28	72	30	63	45
	Cornus alternifolia L.f.	14	86	7	44	38
	Corylus cornuta Marshall	22	78	63	88	69
	Lonicera canadensis Marshall	15	85	7	44	37
	Maianthemum canadense Desf.	38	62	56	81	50
	Oryzopsis asperifolia Michx.	28	72	41	75	54
	Osmorhiza claytonii Michx.	19	81	15	50	41
	Ribes cynosbati L.	0	100	0	25	25
	Rubus pubescens Raf.	27	73	48	88	64
	Tilia americana L.	16	84	22	56	47
	Trientalis borealis Raf.	11	89	11	44	39
	Ulmus Americana L.	13	87	4	25	22
	Uvularia sessilifolia L.	21	79	11	38	30

Table 4a. ANOVA and TKHSD means comparisons for Richness and Evenness in disturbance categories Landing (L), Skid-trail (S) and Off (O) grouped by season of harvest (summer vs. winter). Different lower-case letters indicate significantly different ($p = 0.05$) means for disturbance categories.

Disturbance	Mean ± SE Summer		n	Mean ± SE Winter		n
	Richness	Evenness		Richness	Evenness	
L	38.63 ± 2.17 a	0.79 ± 0.04 a	8	41.67 ± 2.38 ab	0.81 ± 0.03 a	9
S	39.0 ± 1.54 a	0.77 ± 0.03 a	16	43.89 ± 1.68 a	0.86 ± 0.02 a	18
O	30.47 ± 1.59 b	0.80 ± 0.03 a	15	37.75 ± 1.78 b	0.83 ± 0.02 a	16
	$F = 8.66$, df = 2	$F = 0.27$, df = 2		$F = 3.17$, df=2	$F = 1.39$, df = 2	
	$P = 0.001$	$P = 0.766$		$P = 0.053$	$P = 0.26$	

Table 4b. ANOVA and TKHSD means comparisons for Richness and Evenness by season of harvest with plots combined for disturbance categories (L and S, O). Different lower-case letters indicate significantly different ($p = 0.05$) means by season categories.

Disturbance	Mean ± SE L and S plots		n	Mean ± SE O plots		n
	Richness	Evenness		Richness	Evenness	
S	38.88 ± 1.38 a	0.77 ± 0.02 a	24	30.47 ± 1.64 a	0.80 ± 0.03 a	15
W	43.15 ± 1.30 b	0.85 ± 0.02 b	27	37.75 ± 1.59 b	0.83 ± 0.02 a	16
	$F = 5.05$, df = 1	$F = 9.42$, df = 1		$F = 10.19$, df=1	$F = 0.80$, df = 1	
	$P = 0.029$	$P = 0.004$		$P = 0.003$	$P = 0.38$	

Table 5. ANOVA and TKHSD means comparisons for standardized aspen regeneration and residual basal area in disturbance categories Landing (L), Skid-trail (S) and Off (O) grouped by season of harvest (summer and winter). Different lower-case letters indicate significantly different ($p = 0.05$) means by disturbance categories.

Disturbance	Mean ± SE Summer		n	Mean ± SE Winter		n
	Regeneration	Residual BA		Regeneration	Residual BA	
L	12.5 ± 15.80 a	2.25 ± 1.36 a	8	19.00 ± 8.88 a	0.67 ± 0.45 a	9
S	12.38 ± 11.17 a	1.63 ± 0.96 a	16	12.78 ± 6.28 a	0.67 ± 0.32 a	18
O	94.19 ± 11.17 b	2.38 ± 0.96 a	16	102.0 ± 6.66 b	0.81 ± 0.34 a	16
	$F = 16.08$, df = 2	$F = 0.17$, df = 2		$F = 53.93$, df=2	$F = 0.06$, df = 2	
	$P = 0.001$	$P = 0.85$		$P < 0.001$	$P = 0.94$	

Figure 1. Plot layout: using the network of skid trails created during the harvesting operation a gradient of disturbance conditions were identified across each site. Relevé plots were placed in areas identified by level of disturbance, one "L" plot was placed in or adjacent to the landing, two "S" plots were placed within skid trails, and two "O" plots were placed off of skid trails and landings.

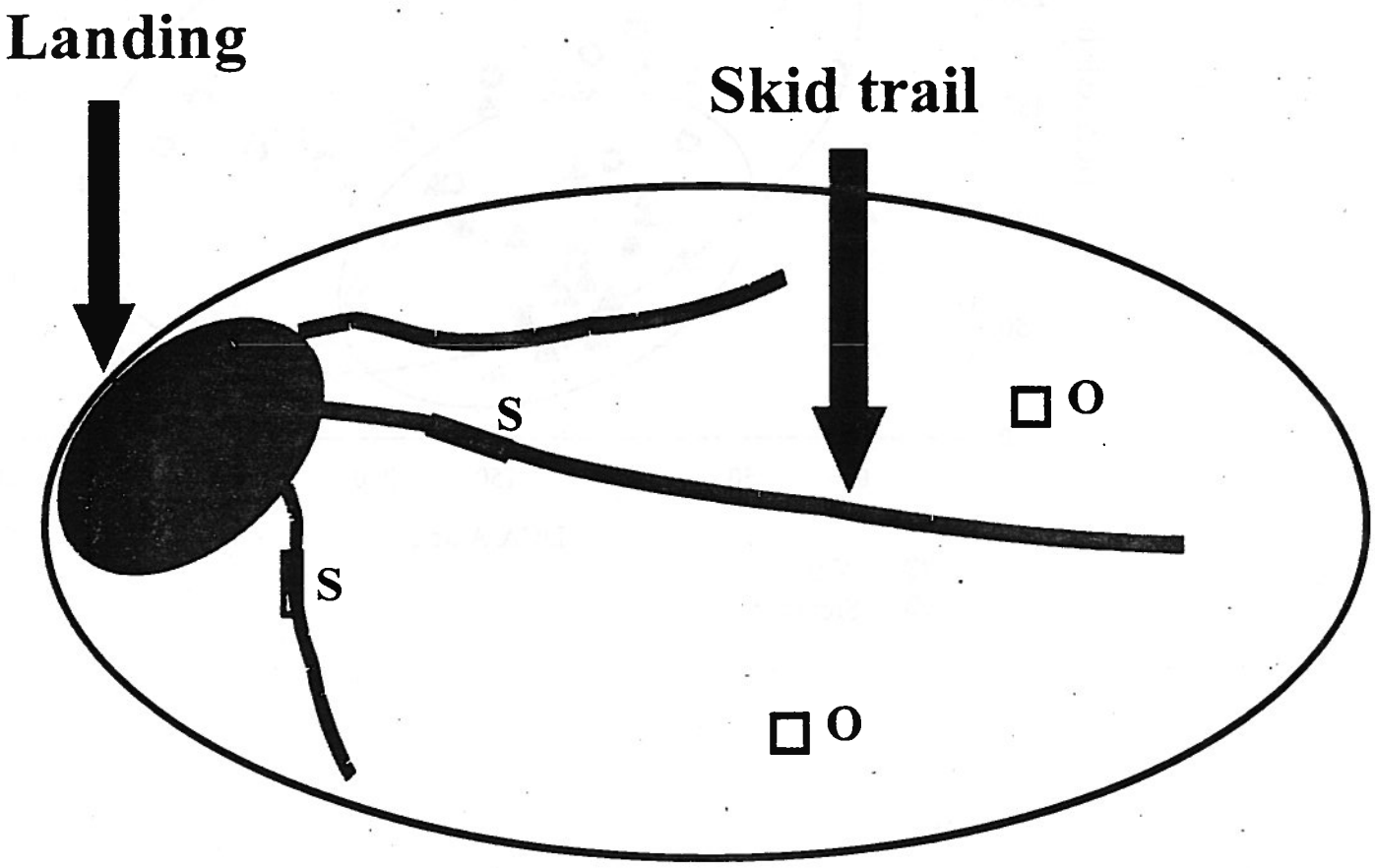


Figure 2a. Detrended correspondence analysis (DCA) of higher disturbance (L and S combined) vegetation plots by season of harvest. Bivariate ellipses represent 95% of data within season of harvest categories.

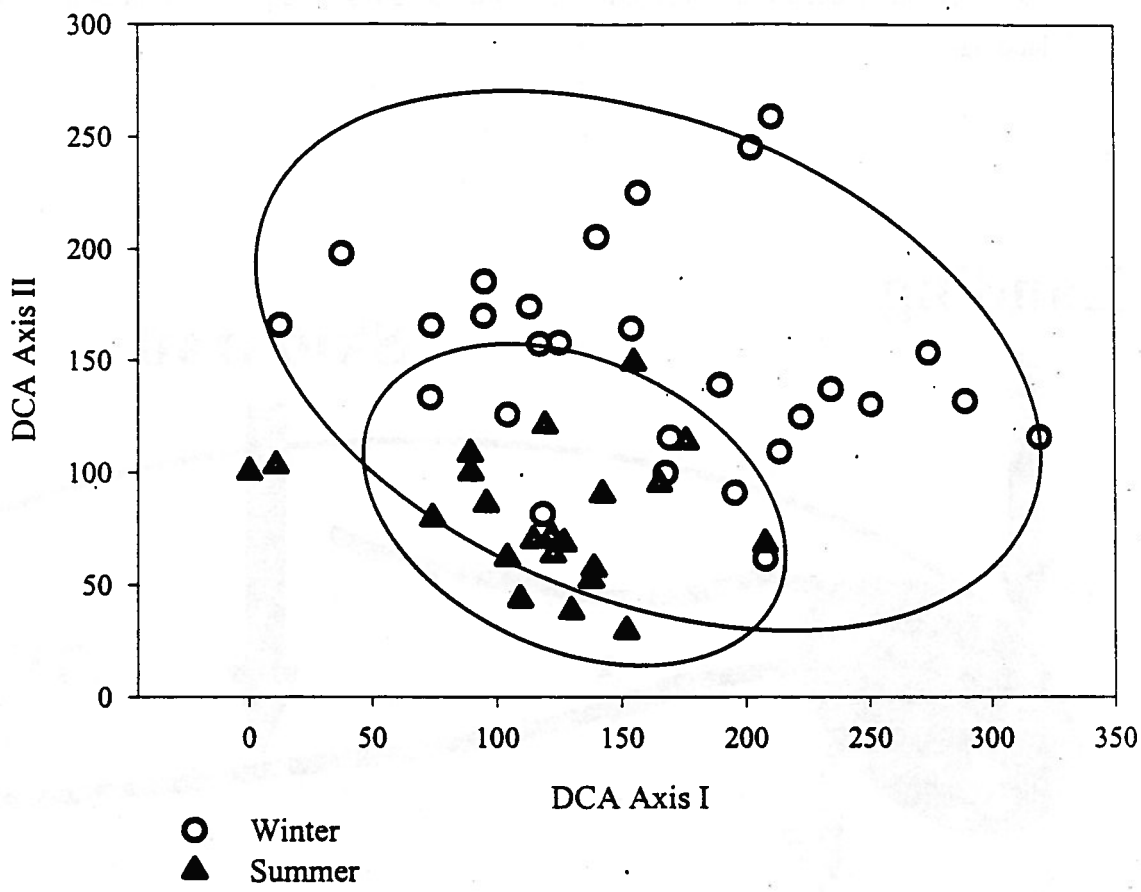
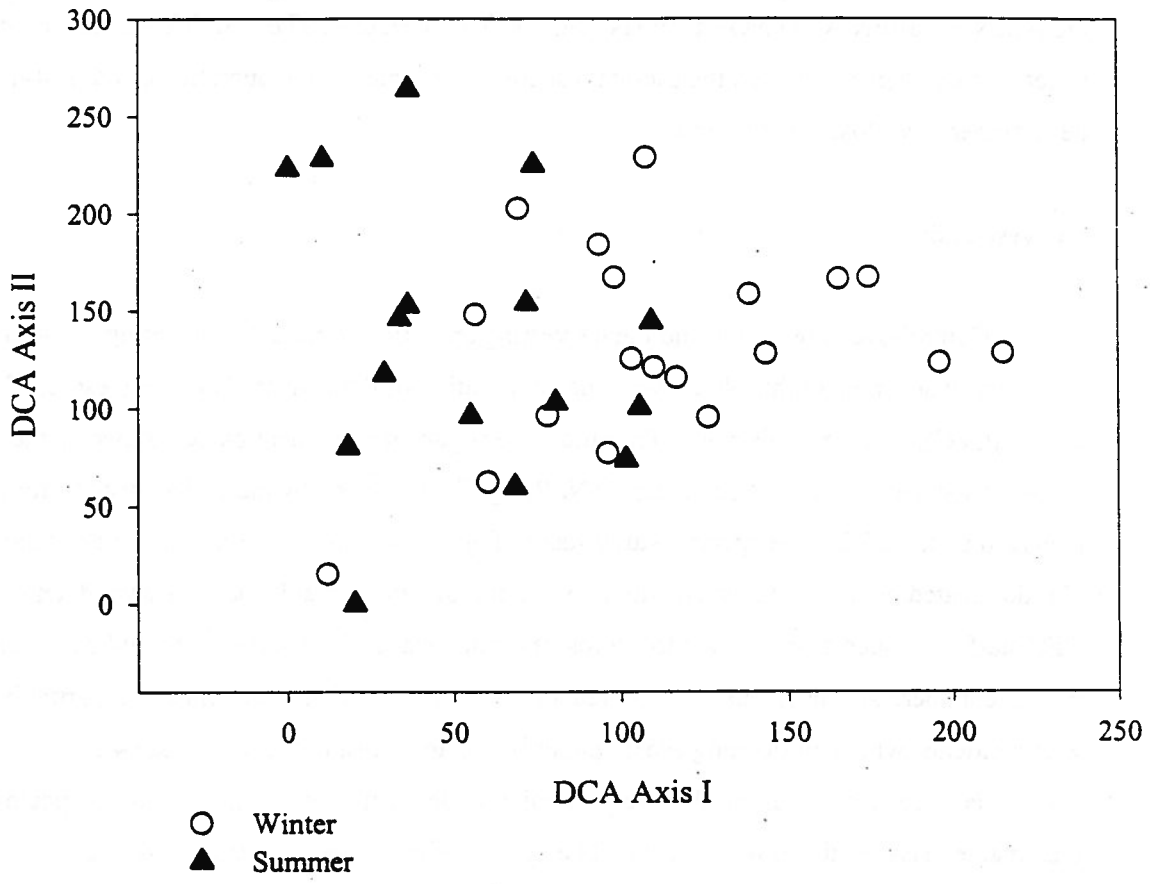


Figure 2b. Detrended correspondence analysis (DCA) of control conditions using off trail (O) vegetation plots to comparing inherent site difference between winter and summer harvested sites.



BOONE SALE - PROJECT STATUS March, 2001

Background

The Boone Sale is a case study that was designed to meet Objective 3 in the proposal: IMPACTS OF HARVESTING ON REGENERATION, PRODUCTIVITY, AND FLORISTIC DIVERSITY OF QUAKING ASPEN AND NORTHERN HARDWOOD ECOSYSTEMS. More specifically the goal was to set up case studies in which the pre-harvest conditions, harvesting operations, and post-harvest development are closely monitored.

Harvest design

Control over site access and the harvesting operation is critical for creating the study conditions necessary to accomplish this objective. The cooperation of the University of Minnesota, Cloquet Forestry Center (CFC), will meet this need. The study site is part of a 160 acre parcel known as the Boone property, located in Sec. 30, Township 55N, Range 21W, owned by the University of Minnesota and managed by the CFC. The specific study stand of approximately 20 acres is a mature stand, 55 to 65 years old, dominated by birch and aspen with a minor component of maple, oak, basswood, and balsam fir. The CFC staff developed a timber sale to harvest the study stand. The harvest was laid out to represent a typical commercial timber sale for this area and stand type, which is a commercial partial harvest clearcut with residuals, where all quaking aspen, paper birch, and balsam fir greater than 4.5 inches DBH were cut. Other tree species were left on the site for habitat or aesthetic objectives. Retained species consisted of oak, maple, basswood and white cedar. The specified harvest system employed was what is commonly referred to as a mechanized "full tree" system, consisting of a feller-buncher, delimber, grapple skidder, and slasher. The timber sale plan for the study stand contained several constraints to ensure accomplishment of the study objectives. As part of the harvest planning process, the landing area(s) were specified based on the geometry and topography of the study stand. This aided in pre-harvest plot selection.

Pre-harvest sampling

Permanent Plots: Upon completion of the sale area map and designation of the landing area(s), thirty 3-m x 20-m permanent plots were established for pre-harvest sampling, one plot on the designated landing area,

22 plots on areas covering the range of disturbance on skid trails ranging from heavily used to only used once or twice, and 7 plots on areas expected to be undisturbed by the harvesting operation. Each plot was permanently located by stake chaser flags securely driven flush into the ground surface with a 12 inch nail on each of the four corners and center of each plot. Red chaser flags are always on the right side of plots heading east towards the de-limbing area and main road. Chaser flags in the center of the plot are orange. All permanent plots were mapped with a Laser Criterion and UTM coordinates for plot centers recorded with the Trimble Pathfinder GPS.

Overstory conditions: Overstory composition and basal area were measured in a 2-m^2 prism plot from each 3-m x 20-m plot center. For trees inside the permanent plots, measurements include azimuth and distance from the center of the plot and DBH. Heights, and crown length (LCR) were measured for two trees per species (randomly chosen). For these randomly chosen trees crown density will be used as an indicator of vigor. Crown dieback was visually classified into three crown density classes (fully leafed, 20 to 50% leaf loss, >50% leaf loss). All trees measured were tagged at the base with round aluminum tags for future sprouting measurements.

Ground vegetation: Ground vegetation was characterized for the 3-m x 20-m plot following the relevé method described in Mueller-Dombois and Ellenberg (1974). Specifically, on each relevé plot, occurrence of all vascular plant species was recorded and placed in a cover class: (1) single occurrence, (2) <5% (occasional), (3) <5% (plentiful), (4) 5-25%, (5) 26-50%, (6) 51-75%, and (7) 76-100%.

Regeneration: 1) Oak regeneration will be monitored on two subplots (1-m x 3-m) located on opposite ends of each permanent plot (60 plots total). Aluminum tags were placed at the base of oak seedlings and height was recorded. 2) Post-harvest birch sprouting will be monitored on the permanent plot. If a permanent plot contained less than 5 paper birch, additional paper birch were selected from outside the plot for measurement to ensure a total of 5 birch were measured per permanent plot. In addition, all yellow birch within a 20-m radius from plot center were measured.

Soils: Soil samples were taken from half sections of each permanent plot with each section located on opposite-cross corners (Fig. 1). This design left a portion of each permanent plot undisturbed by sampling in order to repeat sampling plots after the harvest. On each half section of permanent plot an average of 20 soil cone penetrometer readings (to 15 cm depth) were taken as a measure of pre-harvest soil strength using the RIMIK CP 20 Cone Penetrometer. Soil samples were collected from the top 15 cm of the soil profile for a subset of 15 plots for soil particle size analysis (Grigal 1973). Bulk density samples were collected

on the same subset of 15 plots. The bulk density samples were taken with both a soil core sampler (Blake and Hartge 1986) and by the irregular-hole method (Howard and Singer 1981). Specifically, on all 15 subplots, four soil cores were taken using a (1131.5 mL) core sampler and on half of these subplots four pits were excavated with variable volumes. Both methods were destructive to the vegetation and therefore each bulk density sample was taken just outside of the permanent plot border (Fig. 1).

Coarse Woody Debris (CWD): CWD was inventoried for each permanent plot. Every log with a large end diameter of ≥ 5.0 cm was given a decay class code as follows: 0 = Recent - bark intact, small twigs present, wood firm; 1 = Moderately old - bark only partially intact, small twigs absent, wood firm; 2 = Old - bark mostly separated from sapwood and sloughed off (except in paper birch), large branches present, wood soft; 3 = Very Old - bark absent or only fragments remaining (except in paper birch); 4 = Extremely old - no wood remains and applies to mounds and pits. Total length of logs occurring within the plot boundary was measured (m) and diameter at the large end of the log was recorded (cm). If species of the log could be discerned it was recorded. Snags ≥ 5.0 cm in diameter were also measured within each permanent plot. Total height (m) and diameter (cm) were taken for each snag (at breast height if possible, other wise at top portion of snag). Similar decay class codes were applied: 0 = Recent - small twigs present, bark whole, may have wilted leaves; 1 = Moderately Old - small twigs still present but no leaves, bark whole; 2 = Old - bark mostly separated from sapwood, large branches present; 3 = Very Old - bark absent or only in fragments (except birch), branches missing, wood unsound. Species was recorded for those snags that could be identified. Stumps were measured as snags in addition to logs that were leaning or propped against other trees.

Harvesting

Harvesting began in the Fall of 1999 but was terminated within one day due to wet conditions. A portion of the landing area was cleared but stumps were not removed or pushed out of the area. The portion of the landing cleared during this operation was mapped using the Trimble GPS. The following summer harvesting occurred from August 9-23, 2000. Weather conditions were dry for most of the harvest with some rain during the second week. The soil was wet enough to cause some diversion of skid trails on steep slopes. A landing area off site previously used by a St. Louis County harvest was used for slashing and loading trees onto trucks. The area previously designated as the landing in the Fall of 1999 was used for delimbing activities and skidder turn around. Some rutting did occur in the delimbing area and entrance to the site but not on most trails within the sale. When possible, only one machine (harvester or

skidder) operated at a time. This constraint was to allow intensive monitoring of each machine as it worked in the stand. When this was not possible (usually due to the need to make faster progress before weather conditions worsened), on the ground notes were collected by field crew positioned at the landing and at points within the stand where operations were taking place (*e.g.* skidder pick up and drop off of log piles). The timber sale specified that felling was to begin from the roadside and work into the stand, constantly opening a larger vista to satellite reception by the GPS system in order to improve the accuracy of the monitoring of the felling equipment. This was achieved for the most part, with some gaps in GPS coverage occurring due to poor satellite positioning (issue of time of day rather than canopy cover). During some of the gaps in coverage, ground notes will aid in filling in equipment traffic patterns. During the harvest, field crew constantly took note of plot conditions (i.e. traffic on plot) and marked any nearby residual tree that would be left as an aid in future location of permanent plots. Soil samples were collected periodically to track soil moisture conditions throughout the harvest. During the harvest, the tree species were noted for all loads.

Post harvest sampling

Permanent plots: In Fall 2000, permanent plots were re-located using a combination of chaser flags, a metal detector to find buried flags, and marked residual trees. If no trace of plot markings was available, the GPS unit was used to navigate to plot centers previously surveyed. Once plots were located, pin flags were used to mark the corners. Soil penetrometer and bulk density samples were taken using the pre-harvest protocol. The extent of skid trails and permanent plots were re-surveyed using the GPS unit (Fig. 1).

Office and Lab work

Soils: Soil penetrometer data for both pre- and post-harvest conditions are entered into a spreadsheet. Soil moisture and bulk density samples from pre-harvest conditions have been processed while post-harvest samples are to be processed this winter.

Analysis goals for the GPS data: The GPS data taken during the harvesting operation, load information, results of the disturbance assessment, soil sample information, and cone penetrometer measurements of soil strength will all be combined into a comprehensive map of impacts to the site caused by the harvesting operation. Several measures of impact (e.g., area in difference disturbance/compaction categories) will be developed. Regeneration and ground vegetation data taken over the span of several years will be

correlated to the impact measurements to develop relationships between site impacts and subsequent productivity of the site.

Data storage and file organization - Trimble GPS data can be accessed in both Trimble Pathfinder format (Pathfinder Office 2.50, Copyright 8 1996-1999, Trimble Navigation Limited) and Microsoft Excel. All 110,926 records have been differentially corrected using the Itasca County base station (URS type) located in Grand Rapids, MN at Lat. 47 14 11.120526 N Lon. 93 31 32.222568 W Altitude 404.891. Separate files, by date downloaded (day of harvest), exist in both formats but have also been combined to create master files by week for the harvesting period (there are too many records to combine into one excel sheet).

Data cleaning and analysis preparation - Gaps in data (i.e. loss of transmission due to satellite coverage or due to both harvester and skidder operating simultaneously) have been identified by time stamp. Date and time stamps will be used to look for notes on where the equipment was located. Once the note is found in the field notebook for a gap in time, an estimate of UTM location will be determined (based on pre-survey data) and added as a new record with notation that it is an estimate rather than a location recorded during the Harvest. For example, first using field notes, a list is made of plots that have been "hit" (have traffic from skidder or feller buncher) by equipment within the time gap in GPS coverage, then second, match the plots to estimated UTM locations for those plots (based on previous survey of plot centers). Attributes for each record will be added from field notes where appropriate (e.g. species of log piles, loaded vs. unloaded).

Post harvest sampling - TO BE DONE next spring and following years*

Harvesting impact: at each permanent plot a team of two observers will make a visual assessment of site effects. Point observations will be made in the center of each plot by identifying the visible layer in a 30-cm circle at each point and evaluating the level of disturbance at the point. Visible layer categories are litter, organic soil, mineral soil, muck, slash, or non-soil. Disturbance categories are undisturbed, trafficked, scarified, gouged, rutted, mounded, covered, or unknown (unknown is only used in the case of heavy slash cover where the conditions of the soil cannot be assessed.)

Residual Overstory: Pre-harvest measurements will be repeated the first and fifth year after harvest. Mortality and vigor (crown density) will be assessed annually. Physical condition of residual trees will

also be noted (if scarred: proportion of stem scarred, diameter of scar and height on the stem). Damage to residual tree crowns will be noted: 1) size of branches broken, 2) % crown damaged.

Ground Vegetation: Ground vegetation will be assessed using the relevé method (as in pre-harvest sampling) yearly during July or August in years one and five for a minimum of five years.

Tree Regeneration: Regeneration measurements on established plots will include number of trees and average and top height for each species (this includes counting number of sprouts per stump for an estimate of density-competition). Origin of tree regeneration (sprouts, suckers, seed) will also be documented. The general condition of stumps will be recorded: 1) proportion of stump driven over, 2) % bark removed, 3) height of stump, 4) diameter of stump and 4) bud bank condition (Tappeiner et al. 1996). Browsing pressure from white tailed deer will be measured as number of browsed stems per stump, or by seedling.

To increase the sampling of regeneration, additional regeneration plots will be established under a range of overstory conditions (various amounts of residuals). In these plots, the total amount of tree regeneration (number of trees/plot) will be counted. The average and top height for each species will be measured each year. In addition, the above measurements will be made for stumps of birch marked pre-harvest. Sub plots for oak regeneration will be re-located and an assessment each oak seedling made (potential categories could be *e.g.* live, uprooted, if rooted-bark intact).

*The exact intensity of measurements, e.g., yearly vs. in years one and five, will be determined by the availability of funds over the next few years.

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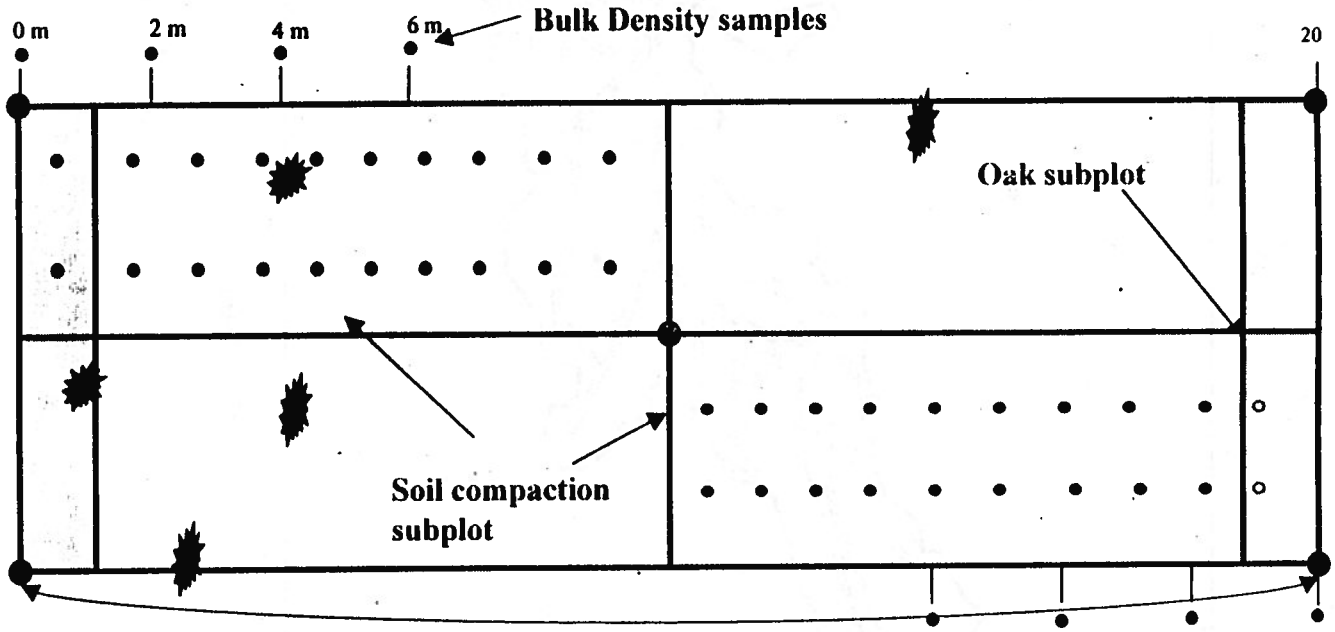
Mueller-Dombois, P., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York, NY. 547 p.

Tappeiner, J. C., J. Zasada, D. Huffman, and B. Maxwell. 1996. Effects of cutting time, stump height, parent tree characteristics, and harvest variables on development of bigleaf maple sprout clumps. Western Journal of Applied Forestry **11**: 120-124.

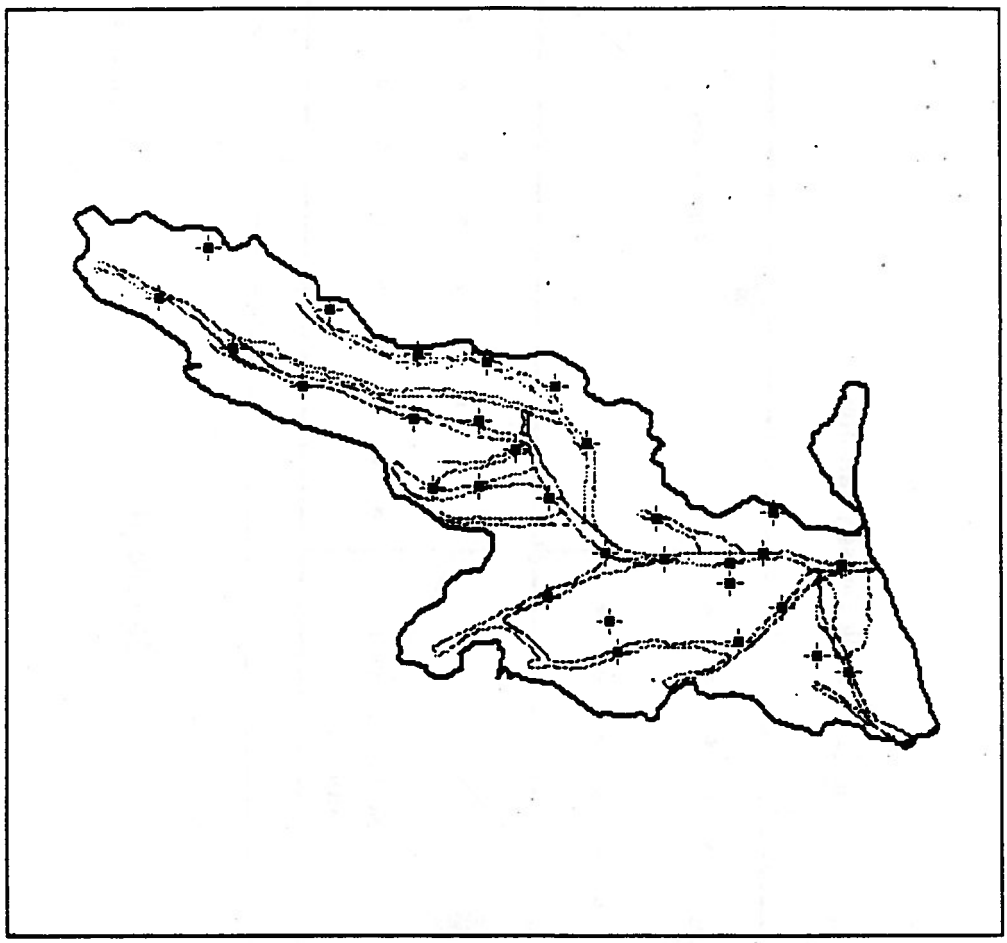
Figure 1. Boone Sale Permanent 3-m x 20-m plot layout*.



Releve plot

*not to scale

Fig. 2. Boone Sale harvest boundary with skid trail boundaries and plot centers as surveyed with the Trimble GPS



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Overstory density and browsing effects on stump sprouting of three northern hardwoods (red maple, northern red oak, and paper birch) in north-central Minnesota.

A PLAN B PAPER
SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL
OF THE UNIVERSITY OF MINNESOTA
BY

Bruce B. Moreira

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
MASTER OF SCIENCE

July 2001

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Stump Sprouting Dynamics and Forest Regeneration

Forest regeneration is a critical component of forest management and conservation. Forest regeneration patterns establish the species composition of a forest. Forest health and species diversity are also determined by regeneration dynamics. Whether a stand is being managed for conservation, harvests, or for multiple uses, understanding and developing the ability to influence forest regeneration is a critical component of forest management.

Forest regeneration is governed by a host of factors at different levels. On a landscape scale, climate, soils, geology, and disturbance have large effects on forest regeneration (Tubbs 1977, Kruger and Reich 1997). Light, moisture levels, nutrient availability, browsing, harvest methods and other factors play significant roles in determining regeneration on a local scale (Pacala et al. 1994). Many of these local scale factors are influenced by overstory density (Groot and Carlson 1996, Messier and Bellefleur 1988, Lieffers et al. 1999, Counte 2000). For example, as overstory density increases, the quality and intensity of light on the forest floor decreases (Messier and Bellefleur 1988, Lieffers et al. 1999). Light quality and intensity is also influenced by the species composition and structure of the overstory canopy (Canham et al. 1994a).

Most deciduous tree species in northern hardwood forests sprout readily from cut stumps and stump sprouts show faster initial growth than seedlings (Johnson and Rogers 1984, Tubbs 1977). Seedling germination and growth have been extensively studied in northern hardwood forest species, but stump sprouting dynamics are not well understood in these species (Crow 1988). Stump sprouts have the advantage of large root systems and carbohydrate reserves from parent trees to accelerate their growth (Johnson 1994).

The role of stump sprouting in unmanaged forests has received little attention. The ability of stumps to sprout after natural disturbances and the frequency of mature trees of sprout origin (i.e. multiple boles) in unmanaged systems indicates that stump sprouting is a significant contributor to tree recruitment in unmanaged forests. In a post-disturbance environment, the faster growth and greater root reserves of stump sprouts gives them an advantage over seedlings and early advanced regeneration to fill canopy gaps (Kruger and Reich 1993). For example, sprout origin red maple were the first trees to reach dominant canopy conditions in unmanaged big-tooth aspen stands and to begin to create a presence in the overstory (Palik and Pregitzer 1992).

In the last century a reduction in the frequency of fire has significantly changed the composition of forests throughout the region (Kruger and Reich 1997). Some species, like sugar maple (*Acer saccharum* L.) and red maple (*Acer rubrum* L.), have increased while others, such as northern red oak, have decreased (Crow 1988, Palik and Pregitzer 1992, Abrams 1998). Red maple has been increasing in dominance across its native range not only because of the absence of fire, but because of red maple's ability to rapidly invade disturbed areas and maintain itself in established stands (Abrams 1998). Northern red oak (*Quercus rubra* L.) has decreased in abundance not only because of decreased fire frequency and competition with fire-intolerant species (Crow 1988) but because of limited success with regeneration efforts, gypsy moth outbreaks, oak decline, and heavy browsing (Johnson 1994). The fact that both species are able to sprout from stumps indicates that a better understanding of sprouting dynamics might improve management efforts for red maple and northern red oak.

Through sprout growth is determined by many of the same factors as seedling growth (i.e. browsing, temperature, available resources), the way sprouts may respond to these factors

and the possible interactions between these factors may differ between sprouts to seedlings. For example, browsing affects seedlings and sprouts. Browsing typically reduces the overall growth of seedlings (Canham et al. 1994b, Saunders and Puettmann 1999b). Deer browsing also slows seedling growth and can tip the balance to competition towards shrubs and unwanted vegetation (Saunders and Puettmann 1999a). Stump sprouts, however, have multiple stems that compete for resources and if browsing were to reduce the total number of competing sprouts on a stump, it would increase the growth of the dominant sprouts (Johnson and Rogers 1984, Lamson 1988, Lowell et al 1989).

Stump sprouting dynamics add a number of factors to regeneration considerations that are not applicable to regeneration from seed. Some of these factors are determined before the harvest or disturbance, such as stump diameter or available carbohydrate reserves. Others, like stump height, are determined by the method of harvest or the nature of the disturbance.

This literature review will examine the current state of knowledge in stump sprouting dynamics and consider implications of those dynamics for forest regeneration.

Factors Affecting Stump Sprouting

The factors affecting stump sprouting can be divided into harvest independent factors and harvest dependent factors. Harvest independent factors are pre-existing conditions which do not depend on the harvest method or intensity. These include stand species composition, stand age, and site quality. Harvest dependent factors are the result of some aspect of the harvest or disturbance, for example, stump height or residual overstory. These factors are directly manipulated during a harvest or the disturbance.

Harvest Independent Factors

Two harvest independent factors which effect regeneration from stump sprouts are the species and tree age/stump diameter. The species can have large effects on the magnitude of sprouting. Most obviously, no conifers in northern hardwood forest sprout. Though most hardwoods sprout, each species has different sprouting probabilities and growth rates. However, the physiological and genetic processes that control stump sprouting are not well understood (Kauppi et al. 1991). In many species, like red and sugar maple, young stumps can have sprouting probabilities of 90% in clear-cut conditions (Mroz et al. 1985). Others species, like yellow birch (*Betula alleghaniensis* Britton), are considered "non-sprouting" in the eastern U.S. (Solomon and Blum 1967). Prolific sprouting species often have more basal buds, less basal bud clustering and/or thinner bark (Mroz et al. 1985, Kauppi et al. 1988).

Species also respond differently to damage and rotting. Most species experience increased mortality after damage to growing sprouts, but the response can vary (Kays and Canham 1991). All species sprout less readily when they reach large diameters, but the "optimum" sprouting size varies between species (Johnson 1975, Mroz et al. 1985). Species not only vary in their ability to sprout, but also in the capacity of their sprouts to become canopy trees (Walters and Yanwey 1990, Sander 1990). Sprouts of red maple often succumb to rotting around the base while northern red oak sprouts frequently grow to be healthy canopy trees (Lees 1981, Johnson 1994).

Stump diameter and tree age are highly correlated but the relationship varies with site and competitive environment. On sites with better growing conditions and with lower density stands, tree trunks will reach larger diameters at younger ages. Most of the effects on stump sprouting are more a result of diameter rather than age, but it is difficult to separate the two. Most authors

treat diameter and age interchangeably (Babeux and Maufette 1994). For clarity, I will treat them as closely related factors with basically similar effects but identify situations which diameter or age may be more directly related to a given effect.

Stump diameter and age can have significant effects on stump sprouting. The magnitudes of the effects varies with the aspect of sprouting vigor. In fast growing short-lived species, like red alder (*Alnus rubra* Bong.), stump sprouting probability declines sharply as trees get older but sprout height and diameter growth have only moderate declines with tree age (Harrington 1984). For long-lived species, neither probability of sprouting nor growth of sprouts have linear relationships with stump diameter and age. Spouting probability tends to remain constant for canopy trees until early maturity after which it declines (MacDonald and Powell 1984, Lynch and Bassett 1987). This decrease can be rapid or gradual depending on the species and the site (MacDonald and Powell 1982, Mroz et al. 1985, Lynch and Bassett 1987). For oak species, the decline seems to be more gradual (Lynch and Bassett 1987) than for maple species (MacDonald and Powell 1982, Mroz et al. 1985). Sprout number does not appear as sensitive to stump diameter as sprouting probability. For most trees, sprout number increases with stump diameter up to a plateau after which it decreases (Mann 1984, Mroz et al. 1985). However, in one study on sugar maple, stump diameter had no effect on number of sprouts (MacDonald and Powell 1983). In contrast to sprouting probability and sprout number, sprout height growth appears to be independent of stump diameter (MacDonald and Powell 1983, Mann 1984, Mroz et al. 1985).

The mechanism behind the relationship between diameter/age of the stump and sprouting probability and vigor has been examined in birch species (*Betula spp.*). Bud development and "bud banks", the reserve of dormant buds around the collar of a tree, are the most likely explanations as to why stump diameter and age appear to reduce sprouting probability. As trees

age, buds tend to develop in tight clusters rather than individually, which reduces the sprouting ability of all buds in the cluster (Kauppi et al. 1987). It is also often cited that older trees also tend to have bark that is too thick for buds to burst through (Mroz et al. 1985, Kauppi et al. 1991). However, the effect of bark thickness has never been tested empirically.

If bark thickness was the only cause of reduced stump sprouting in larger trees, species like northern red oak, which has a very thick bark, would be expected to be more affected than a species like red maple, which has thinner bark. However, large northern red oak can have sprouting rates as high as 60% (Lynch and Bassett 1989), similar to the sprouting rate of large red maple (Mroz et al. 1985). Without measuring bark thickness and sprouting percentages, it is difficult to conclude whether or not bark thickness effects sprouting.

The larger root systems and more trunk area for bud development would be expected to increase sprout number and/or growth in larger stumps. Mroz et al. (1985) found this to be true only for total sprout biomass. Stump diameter had no effect on height growth of the tallest sprout. Two comparable studies on sugar maple and red maple found no increase in sprout vigor in larger stumps (Mann 1984, MacDonald and Powell 1983), though they made similar or identical measurements to Mroz et al. (1985). The lack of a benefit of a larger root system could be because the growth of the sprout is not resource limited or that another factor related to stump diameter and age is working to counter-act the positive effect of added resources.

Harvest Dependent Factors

Sprouting success is also dependent on how a tree is harvested and the resulting growing conditions. Some effects are direct, for example, shorter stumps results in fewer buds which result in fewer sprouts. Some effects are indirect, for example, leaving more residual trees decreases resource levels, which then decreases growth rates of sprouts. Many effects of

harvesting have the potential for interaction with other harvest dependent and harvest independent factors.

Stump height can have a significant effect on stump sprouting. Since the dormant basal buds that develop into sprouts are located on the side of a stump, taller stumps could be expected to have more sprouts. In some cases, taller stumps have more sprouts than shorter stumps during the first few years of growth because the taller stumps have more area on the side of the stump for dormant basal buds to develop and subsequently sprout (Harrington 1984, Tappeiner et al. 1996, Jobidon 1997). In other situations, stump height appears to have no effect (Ducrey and Turell 1992, Johannson 1987). As the stems grow, self-thinning reduces the number of remaining stems and the differences in the number of sprouts between short and tall stumps disappear (Jobidon 1997). Stump height does not appear to effect sprout vigor (Ducrey and Turrell 1992, Jobidon 1997). Therefore, although shorter stump height appears to reduce the initial number of stems on a stump in some cases, it does not affect the long-term viability of stump sprouts in most situations. In areas with heavy browsing or pest attacks, taller stumps may increase the long term survival by increasing the number of viable stems at a young age and thus increasing the probability that one or more of the stems would survive browsing or insect attacks to become mature trees.

The location of the buds (i.e. above vs. below ground) influences sprouting levels. In pubescent birch (*Betula pubescens* Ehrh.) in field sites, 90% of the dormant buds were below ground, but only 10% burst, while above ground 40% of the buds burst (Kauppi et al. 1988). In a longer-term growth study with silver birch (*Betula pendula* Roth) saplings, Kauppi et al. (1991) found that a higher proportion of above-ground buds contributed to the sprouting of saplings despite more buds being underground. Lowering the ground level around coppiced saplings was

found to be the most effective way to increase sprouting, partially because of increased light, but also because of other environmental factors associated with ground level.

Canopy conditions have a range of effects on understory conditions (Leak and Solomon 1975, Tubbs 1977, Lieffers et al. 1999, Counte 2000). Increasing residual overstory has been shown to decrease stump sprouting in shade tolerant and shade intolerant species (Church 1960, Tappeiner et al. 1996, Gardiner and Helming 1997, Comeau et al. 1998). Stumps of understory big leaf maple (*Acer macrophyllum* Pursh.) cut under a closed canopy had a low rate of sprouting. Once the canopy trees were harvested, the rate of sprouting in big leaf maple increased dramatically, even in stumps that began sprouting two years before the harvest (Tappeiner et al. 1996). In red maple, canopy release of 7-year-old stumps significantly increased DBH growth of sprouts, but did not significantly increase height growth (Trimble 1974). Red maple and gray birch (*Betula populifolia* Marsh.) sprouts showed increases in basal area growth with increased light (Kays and Canham 1991). A comparison of stump sprouting in water oak (*Quercus nigra* L.) under two densities of residual overstory found that stumps have higher survival and growth after greater overstory removal (Gardiner and Helming 1997). Paper birch (*Betula papyrifera* Marsh.) had a similar response to reduced overstory densities (Comeau et al. 1998). The sprout growth of paper birch was equal, under heavy versus light thinning treatments, but under a clearcut treatment, sprouts had higher survival and were taller after two years.

Two studies, one on water oak (Gardiner and Helmig 1997) and one on paper birch (Comeau et al. 1998), were similar enough to allow comparison in the response of two species to overstory density. Gardiner and Helmig's (1997) findings agree with Comeau et al.'s (1998) findings, though Comeau's found a stronger effect of overstory density on sprout growth (40%

vs. 25%). The difference may be a result of Comeau et al.'s treatments having larger difference in density (600 stems/ha vs. 210 stems/ha in Gardiner and Helmig). Comeau et al.'s (1998) findings suggest that if water oak had been measured under clearcut conditions, it would have resulted in an even higher rate of sprouting. A wider range of overstory densities may have also overcome the variability that resulted in the seventh year loss of significance in Gardiner and Helmig's (1997) study.

Greenhouse studies have looked directly at the effects of light and temperature, two factors affected by overstory density. Increased light and increased temperature result in increased sprouting, supporting the field studies on canopy density. In greenhouse conditions, increased temperature had a large positive effect on the height of stump sprouts under all light levels in silver birch seedlings (Johansson 1986). The effect of light levels on sprouting depended on temperature. All stumps were tall in high temperature (24° C) and short in low temperatures (12° C) regardless of light levels. In medium temperatures (18° C), increasing light levels from 25 $\mu E/m^2s$ to 400 $\mu E/m^2s$ increased sprout growth over 300% (Johansson 1986). Under controlled garden experiments using European birch (*Betula pubescens* Ehrh.), shading significantly decreased sprout biomass and height growth (Johansson 1987). Sprouts grown in 10% of full sunlight had less than 25% of the biomass of sprouts grown under 50% sunlight or full sunlight.

The response of stump sprouts to increased nutrient levels is not clear. Mroz et al. (1985) believed that fertilizer augments sprout growth but found that the variation in sprout response to fertilizer was too high to document this. On sites with higher site indices, sprouting percentage was actually lower (Mroz et al. 1985). This may have been because the larger trees on the high quality sites had thicker bark, reducing their sprouting ability. Sprout height,

however, was positively correlated with stump diameter and site quality, supporting the hypothesis that the probability of sprouting depends on physiological factors while the vigor of sprouts depends on environmental factors.

The time of year a tree is cut can also have a significant effect on sprout development, but studies show that the magnitude of the effect is small and the variability is very large. In balsam fir-paper birch forests in Quebec, red maple stumps cut in May had more sprouts than trees cut in June, but the effect was only marginally significant (Babeux and Mauffette 1994). In this study, cutting time had no effect on sprout height and biomass growth and after two growing seasons, any effects of cutting season were gone. As a result, Babeux and Mauffette (1994) concluded that other factors beside cutting season should be examined to manage the level of stump sprouting in red maple. This conclusion was supported by a similar study on four hardwood species by Kays and Canham (1991). The study found that cuts before and after the growing season yielded significantly more and taller stumps after two years, but the effect was non-significant after three years. The roots reserves of the stumps recovered quickly, showing that the effect of cutting time was short-lived. Johansson (1992) found similar results in two Scandinavian birch species. Winter cuts resulted in both taller and thicker sprouts than cuts during the summer months. Harrington (1984) found that winter cuts had lower mortality in red alder sprouts, but only 10 to 15%. Johansson (1992) and Harrington (1984) did not measure sprouts for sufficient time to determine if the effect was short-lived.

When root reserves as well as sprout growth are examined, a more complete picture of the effects of cutting time on tree growth emerges. Kays and Canham (1991) examined the effect of harvesting on root reserves and sprout growth in saplings of four hardwood species in New York. They found pruning early in the growing season and pruning multiple times during

the growing season significantly reduced the root reserves of stumps. The intensity of the reduction was very different between species but the overall impact was the same for all species. When tree growth was measured, the effect of cutting time on tree growth was smaller and became negligible after three growing seasons. It should also be emphasized that this study was conducted on sprouts growing from sapling stumps and the objective of cutting the sprouts was to reduce sprout regeneration. Adult trees may not be affected as much by the reduction in root reserves because they have much larger reserves.

The rate and dynamics of self-thinning of sprouts on a maturing tree can have a large effect on surviving sprouts. Each stump has multiple sprouts but each sprout cannot be considered an individual because they are connected to the same root system. As stumps age, the number of sprouts declines until only one, or in most cases a few, dominant sprouts remain to grow into an adult tree. This process of self-thinning has been seen for a diverse range of species (Haney 1962, Wendel 1975, Beck 1977, Johnson and Godman 1983, Lamson 1988). In many cases the process of self-thinning decreased the sensitivity of overall sprout growth to other factors which may have reduced sprout growth in the short term (e.g. stump height in Jobidon 1997). Most studies did not monitor the sprouts long enough to discover if self-thinning would weaken or eliminate any of the effects of other factors on sprout growth over the long term. The extent of self-thinning questions the final relevance of many of the factors discussed above, especially when considering their effect on the number of sprouts per stump. If a clump of stump sprouts is ultimately reduced to one or two sprouts, the end effect of a 50% reduction in the initial number of sprouts may be negligible. Total sprout biomass also could be of questionable importance. Other factors would not be effected by self-thinning. For example, the percentage of stumps sprouting and measurements associated with the tallest sprout are not

reduced by self-thinning. The tallest sprout after 5 years usually is the surviving sprout after 25 years (Lowell et al. 1989).

Competition between sprouts on a single stump can also affect stump sprout growth and success. Reducing the competition between sprouts by manually thinning smaller stump sprouts increases the growth of the remaining sprouts (Johnson 1975, Lamson 1988, Lowell et al. 1989). Competition between sprouts could interact with a number of other factors to compound or counteract their effect on sprout growth. The competition can be more intense in poor growing conditions than in good ones (Wilson and Tilman 1993). Sprouts growing in dense clumps (i.e. with high competition for resources) would be more negatively affected by dense overstories or low nutrients. None of the studies on stump sprouting examined competition of sprouts with respect to environmental conditions. Competition could also interact with browsing to compound the negative effect of browsing (e.g. browsing could deplete the total resources available to competing stems, reducing the overall growth of the sprout) or to counteract the negative effect of browsing (e.g. by reducing competition between the sprouts, browsing could increase growth of the tallest sprout).

Management of Stump Sprouting for Timber

Stump sprouting has been managed for pulp and fuelwood production around the world for centuries. Though, not as common, stump sprouts can also be effectively used for timber production in northern hardwoods. Research on timber production in northern hardwoods has focused on northern red oak but any sprouting species could, in theory, be managed for timber. Most studies have concentrated on thinning stump sprouts to a single dominant sprout to reduce competition between sprouts on the same stump. For northern red oak, the earlier a stump is thinned the greater the effect of thinning on the size of the tree (Johnson 1975, Johnson and

Rogers 1984). Equations have been developed from a 25-year study of northern red oak sprout growth that predict the diameter of a thinned northern red oak stump sprout in Wisconsin (Johnson 1975, Johnson and Rogers 1984). If thinned after 5 years, DBH at age 25 was 27 cm compared to 16 cm for an unthinned clump, a 69% increase. The increase was similar on good, medium, and poor sites. A similar study on red and white oak (*Quercus alba* L.) in Missouri found a 2-3 fold increase in survival but only a 25% increase in average DBH 25 years after thinning treatments were applied to oak stems (Lowell et al. 1987). A later study (Lowell et al. 1989) in a clear-cut northern red oak and white oak (*Quercus alba* L.) stand found a 55% increase in bole volume of thinned sprouts vs. unthinned sprouts. All four studies agree that the earlier a stand is thinned, the greater the increase in growth. Other sprout thinning methods, such as 2,4-D or Triclopyr application, have been found to be as effective as mechanical thinning in reducing sprouting to a dominant stem (Groninger et al. 1998).

Stump sprouting trees can retain multiple stems and still remain healthy in maturity. Only one study examining stump thinning considered the basal area of the stems that were cut and the loss in yield from their removal. In white oak, the tallest sprout in thinned sprouts grew significantly larger than the tallest sprout in unthinned sprouts, but when all sprouts (including the removed sprouts) were taken into consideration, unthinned sprouts had over twice the volume and nearly twice the volume growth of thinned sprouts after 25 years (Haney 1962). The trees in the study were growing on poor to fair soils (60 S.I.), which may have restricted the ability of stump sprouts to take advantage of thinning. Haney (1962) thinned sprout clumps at age 25, i.e., after the sprouts have already undergone the majority of the self-thinning. This may have decreased the ability of sprouts to take advantage of the reduced competition, since the most intense competition and self-thinning had already occurred. Even with these limitations, the

results call attention to the tree volume removed by thinning and indicate that it merits consideration in silvicultural applications which focus on total volume more than on volume of single trees.

Sprout thinning in species other than oaks has not been found to have clear benefits to growth. Ten years after thinning basswood (*Tilia americana* L.), black cherry (*Prunus serotina* Ehrh.), northern red oak, and red maple, thinning and pruning treatments failed to increase sprout growth (Lamson 1988). Thinning and pruning stems increased the overall survival probability but didn't significantly increase DBH or height for most species. Basswood and red maple had significant increases in growth 10 years after thinning and pruning treatments, but northern red oak and black cherry did not. However, other studies found large effects of thinning on growth in northern red oak (e.g. Johnson and Rogers 1984, Lowell et al. 1989).

Sprout thinning treatments increase the growth rate of northern red oak stump sprouts, but are also costly. Actively managing stump sprouts for increased timber volume by manually thinning sprouts has not been found to be cost effective in northern red oak (Dwyer et al. 1993). The thinning costs are not compensated for by increased timber yield, even using a conservative 3% interest rate and the maximum market price for timber. However, alternatives to mechanical thinning (e.g. stem herbicide injection, stem spraying) have a much lower application cost (65-40% decrease in Groninger et al. 1998) which could make sprout thinning more cost effective. The margin in Dwyer et al. (1993) that caused thinning not to be cost-effective was small enough that the 40% decrease in thinning costs found by Groninger et al. (1998) would be expected to make sprout thinning profitable. It should also be remembered that profitability considerations were for oak, a high value timber tree with a strong response to sprout thinning, and that the cost

effectiveness of thinning would be lower for trees with lower value or with poorer responses to sprout thinning.

Stump sprout production may not have the potential for complete stand regeneration in many cases (Johnson 1994) but stump sprouts can be used to supplement seedling and advanced regeneration (Wendel 1975). By taking advantage of the natural sprout regeneration after harvest and manipulating sprouts to maximize growth, stump sprouts can add to timber production.

Control of Unwanted Stump Sprouting

Stump sprouts can also be unwanted side effects of harvest operations. Undesired sprouting species can compete with planted seedlings, advanced regeneration or sprouts of the desired species in a stand. Controlling stump sprouting can be a difficult task largely for the same reasons stump sprouting is effective for forest regeneration (i.e. rapid growth of sprouts and high probability of sprouting). Sprout control often uses the same methods as management of stump sprouting described in previous section of this paper (e.g. cutting time and stump height). Indeed, many of the studies cited in previous discussion about cutting time and stump height aimed to reduce sprouting, not to promote it. Other sprout control tactics share methods with sprout thinning, (e.g. herbicide use), though the research efforts are different.

Controlling stump sprouting by cutting during the growing season has been found to be effective for only a limited time period if at all (Babeux and Mauffette 1994, Wendel 1975, Kays and Canham 1991, Ducrey and Turrell 1992, Johansson 1992). A two-year study in Quebec on red maple (Babeux and Mauffette 1994) concluded that cutting during the growing season was largely ineffective at sprouting control and that other means should be used. Reductions in growth and increases in mortality were found in four eastern hardwood species especially for

multiple cuts in one season (Kays and Canham 1991). The same study, however, found that root reserves returned to uncut levels within one or two years, indicating that sprout growth might recover as well. Cutting multiple times during one season increases mortality, thus reducing the number of sprouting stumps in the long term, but may not reduce the long-term growth of the surviving sprouts. The study only covered three years, limiting the possibility to observe long-term effects. The magnitude of the effect of cutting during the growing season is also extremely variable (Johansson 1992) and site and species dependent (Babeux and Mauffette 1994).

Cutting stumps shorter to reduce stump sprouting has also shown mixed results. Greenhouse studies found that taller stumps had more viable buds and more sprouting (Kauppi et. al 1988, 1991). Laboratory studies found significant declines in sprout growth on short stumps (Johansson 1991, 1992), but studies on the same species in the field failed to show the same decline (Johansson 1992). Big leaf maple sprouted more from 60 cm stumps than 30 cm stumps (Tappeiner et al. 1996), but other longer term and more comprehensive studies on other maple species found no significant difference in sprout growth between stump heights (Jobidon 1997, Mroz et al. 1985). Much like cutting season, the reduction in growth achieved by cutting stumps shorter seems to disappear over time in the field (Jobidon 1997).

Chemical and biological control of sprouting has resulted in much more consistent and effective reduction in sprouting rates. Two types of chemical herbicides reduced sprouting by 50% in two oak species during the first year of treatment, but the effect only lasted one or two years (Ward and Bowersox 1979). Fenuron was more effective than 2,4,5-T, but both reduced sprouting. After 14 years, sprout number per stump of treated stumps was half to a third of untreated stumps. In surviving stumps, neither herbicide reduced height growth, however. A similar study on paper birch and pin cherry found comparable results (Jobidon 1998). Chemical

(glyphosphate, bialaphos) applications were found to be very effective in reducing number of sprouts per stump and increasing mortality of stumps, but not in reducing the height of surviving sprouts. Biorational control agents, fungal secondary metabolites, were only effective in some of the cases, signifying the unreliability of the production process. Moritz (1999) also found significant reductions in mean height and number of sprouts on stumps of northern red oak, paper birch, sugar maple and box-elder (*Acer negundo* L.). However, the study only followed sprout growth for two years.

Increased stump mortality is an effective control of sprouts even if the growth of the surviving stumps was not reduced. Given the amount of self-thinning that occurs in stump sprouts (Mroz et al. 1985, Gardiner & Helming 1997, Johansson 1987), reducing sprout number may not be as important since self thinning will reduce sprout number nonetheless. Indeed, reducing the total number of sprouts on a stem could actually increase the vigor of the remaining stems (Johnson and Rogers 1984).

Conclusions

Stump sprouting dynamics are affected by harvest independent and dependent factors. These factors have been studied in a number of different species and in a range of environments. The effects of tree species and stump diameter are independent of harvest methods. The species of a tree can have a large influence on sprouting probability and growth. Larger diameter stumps appear to have lower sprouting probabilities, but larger stumps appear to support sprout growth as effectively as small diameter stumps. While many factors which depend on harvest methods and post-harvest stand conditions may have substantial effects on sprout growth, the two most significant factors to consider when managing for forest regeneration, are overstory density and

competition between sprouts. Browsing is also a major concern but little work has been done examining the effect of browsing on sprout growth.

The majority of the factors influencing sprouting have been examined for only a few species (e.g. the increase in growth after sprout thinning in northern red oak), and few of these factors have been examined over a longer time period. Interactions between factors, such as competition between sprouts and overstory density, also lack extensive examination. As a result, stump sprouting dynamics are not well understood for the majority of the species in northern hardwood forests. Some aspects of sprouting dynamics, like canopy density, have been found to have significant and lasting effects under all conditions, while others, like stump height, have been found to have limited or temporary effects. Sprouting dynamics in unmanaged systems after natural disturbances are also poorly understood.

Successful management of stump sprouting for timber production in northern red oak shows that stump sprouts can be a significant and valuable contribution to a regenerating stand (Johnson and Rogers 1984). Intensive management may not be wise for all species and regeneration goals (Dwyer et al. 1993), but regeneration from sprouts can often be successful with less management than planting or natural regeneration from seed. With a better understanding of sprouting dynamics, forest managers will be able use natural regeneration, from seeds and from sprouts, to more effectively increase productivity and maintain healthy forests. A more complete picture of sprout dynamics will also help predict changes in unmanaged systems after disturbance and help explain landscape level changes in forest composition in species such as red maple and northern red oak

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Chapter 2:

Overstory density and browsing effects on stump sprouting in northern hardwood forests

Abstract: Stump sprouting is a potentially viable, but often overlooked, means of regeneration in managed northern hardwood forests. Two of the most important factors affecting forest regeneration in these forest types are overstory density and browsing. Overstory density and browsing have been widely studied for seedlings and saplings, but less so for stump sprouts. I investigated how stump sprouting after harvest of northern red oak (*Quercus rubrum* L.), red maple (*Acer rubra* L.), and paper birch (*Betula papyrifera* Marsh.) is affected by canopy density and by browsing from white-tailed deer. I measured 5- to 8-year-old stumps on seven sites in Pine and Itasca counties, Minnesota, in stands with residual basal area ranging from 0-40 m^2/ha. Total height, previous year's height growth and D.B.H. of the tallest sprout on each stump were measured, as well as average height of all sprouts, number of times apical dominance was broken (interpreted as browsing even on the tallest stem), and basal area of the residual overstory. All three species had similar responses to residual overstory and browsing, though significant differences between species and sites were present. Residual overstory had a strong negative effect on height and D.B.H. of the tallest sprouts. Height of tallest and average height of stump sprouts appear to be less sensitive to residual basal area than D.B.H. of the tallest sprout. Browsing intensity had a negative effect on height and D.B.H of the tallest stump sprout. Red maple sprouts grew more than northern red oak sprouts in open and closed canopy conditions, but the difference between open and closed conditions for red maple sprouts was larger than for northern red oak sprouts. There was also a high degree of variability in the response of sprouts to overstory density between the sites. The results indicate that leaving residual overstory after harvest, especially in combination with deer browsing, will influence growth of sprouts, and thus the species composition of the future stand.

Introduction

Successful forest regeneration depends on effective silvicultural practices and an understanding of stand regeneration dynamics. Silvicultural practices in Minnesota are promoting more diverse forests and have become more dependent on natural regeneration (Puettmann and Ek 1999). The majority of the dominant species in northern hardwood forests can regenerate from stump sprouts and seeds, which means that natural regeneration in harvested areas may not only come from seedlings. Vegetative reproduction is common in unmanaged forests (Palik and Pregitzer 1992) though the extent and dynamics of sprouting in unmanaged forests is not well established. Vegetative reproduction is widely used for management of aspen (*Populus tremuloides* Michx.) in North America and for fuel and pulpwood production around the world. Regeneration of northern hardwoods, however, relies mainly on mainly on seeds and advance regeneration. As a result, stump sprouting in northern hardwood forests is not well understood. To better manage hardwood regeneration, a better understanding of the dynamics of stump sprouting in relation to harvest practices and other factors is required.

As forest management in northern hardwood forests leaves more residual trees in the landscape (Puettmann and Ek 1999), understanding the effect of the residual canopy on forest regeneration becomes increasingly important. Increased canopy cover can effect a number of understory conditions, such as decreased light levels and quality (Messier and Bellefluer 1988, Lieffers et al. 1999), increased soil moisture tension (Counte 2000), decreased frost incidence (Groot and Carlson 1996), reduced air temperature fluctuations (Counte 2000), reduced soil temperatures (Caldwell et al. 1995), and increased relative humidity (Brand 1986). The density and crown condition of canopy trees directly effects the amount of light reaching the understory (Lieffers et al. 1999). Canopy species composition also effects understory light conditions.

Shade tolerant hardwoods tend to have deeper crowns than light demanding species which reduce light levels in the understory beneath them to lower levels (Canham et al. 1994a). Drought stress under open canopy conditions is a result of higher peak demands on moisture levels, whereas in closed canopy conditions drought stress is more often because of increased competition (Childs and Flint 1987, Mitchell and Arnott 1995, Canham et al. 1996).

A great deal of research has been conducted on the response of seedlings and saplings to overstory density and condition (e.g., Pacala et al. 1994, Messier et al. 1999), but little work has been done on sprouting. Some aspects of sprout growth are expected to be similar to seedlings and saplings. For example, studies conducted on stump sprouts and overstory density have found a decrease in sprout vigor under increased canopy density (Church 1960, Tappeiner et al. 1996, Gardiner and Helmig 1997, Comeau et al. 1998). Other factors, like competition between stump sprouts and root reserves from the parent stump may change stump sprout response to overstory density and condition.

Investigations into the stump sprouting dynamics need to consider factors that are not relevant in regeneration from seed. Some of these factors do not depend on harvest methods or disturbance types, e.g. tree species, stump diameter, and site quality. Though the majority of northern hardwoods are capable of sprouting, the success and vigor of sprouting varies widely between species (Solomon and Blum 1967, Mroz et al. 1985). As stumps age and increase in diameter, the probability of sprouting decreases because of bark thickness and bud clustering (Kauppi et al. 1987, Kauppi et al. 1988). Actual sprout vigor, however, can remain high, even in large diameter trees (Lynch and Bassett 1987, Mroz et al. 1985) indicating that once a bud successfully emerges, sprouts can thrive on larger diameter trees. A factor related to stump diameter is site quality. Site quality can effect the relationship between diameter and age of

stumps, which can result in higher quality sites actually having lower sprouting probability because of thicker bark (Mroz et al. 1985).

Many sprout-specific factors depend on harvest method or disturbance type, such as harvest season and residual overstory density. Stumps on sites harvested in winter tend to sprout more vigorously than stumps on sites harvested in summer because stumps have more carbohydrate reserves in their roots to support sprout growth (Kays and Canham 1991, Johansson 1992, Babuex and Mauffette 1994). However, studies on the impacts of harvest season on sprouting have all been conducted on saplings. It is widely accepted that stump sprouts grow faster than seedlings because of larger root reserves (Johnson 1994). Larger trees would be expected to have larger root reserves, but how much larger the reserves are and for how long the larger reserves effect the growing sprouts is unclear. Reducing the number of sprouts on a stump increases the overall growth of the dominant stump sprouts (Johnson and Rogers 1984, Lowell et al. 1989) but the possible interaction between browsing on smaller sprouts and increased growth of the dominant sprouts has not been examined. Two of these factors, overstory density and browsing, have been cited as central factors affecting forest regeneration in the Lake States (Buckley et al. 1998), but the two factors have not been examined in the same study for stump sprouts.

Three prominent sprouting species in northern hardwood forests in Minnesota are red maple (*Acer rubrum* L.), northern red oak (*Quercus rubra* L.), and paper birch (*Betula papyrifera* Marsh). The presence of red maple in northern hardwood forests has increased from a relatively minor component of the canopy to a ubiquitous tree in early and late successional forests because of the decrease in the abundance of fire across the landscape (Palik and Pregitzer 1992, Abrams 1998, Tift and Fajvan 1999). Northern red oak, on the other hand, has proven

difficult to regenerate by natural or artificial methods because of damage by gypsy moth (*Lymnantria dispar* L.), oak decline, competition from fire-intolerant species, frost damage, and deer browsing (Crow 1988, Johnson 1994, Buckley et al. 1998). Paper birch has remained a relatively stable component in northern hardwood forests over the last hundred years as a pioneer species (Perala and Alm 1990a).

The three species were chosen to represent a shade tolerant species (red maple), intermediate shade tolerant species (northern red oak) and shade intolerant species (paper birch). Red maple and northern red oak comparisons are also important given the rise of red maple and the decline of northern red oak in response to changes in the post-settlement landscape (Abrams 1998, Buckley et al 1998). To better understand the dynamics of stump sprouting in northern hardwood regeneration, my study examined the response of sprout size and growth of three northern hardwood tree species (red maple, northern red oak, and paper birch) to changes in overstory density and browsing.

Materials and Methods

Study species

The three species used for this study, red maple, northern red oak, and paper birch, are common overstory trees in hardwood forests of Minnesota.

Red maple is the most prolific stump sprouting tree and widespread species of the three species in the study (Walters and Yawney 1990, Solomon and Blum 1967). It grows from Florida to southern Canada and from the eastern seaboard to the eastern edge of the Great Plains. It is considered shade tolerant and has been called a "super-generalist" for its function as a pioneer and a climax species (Abrams and Kubiske 1990, Abrams 1998). Sprout regenerated red

maple is often a less desirable timber species than northern red oak or paper birch because bole clumps commonly rot at the base, reducing their size and the quality of the timber (Johnson 1975).

Northern red oak also sprouts readily and is an important timber species (Lowell et al. 1989, Johnson 1994). Northern red oak grows from the central U.S. to southern Canada, farther north than any other oak. It is considered an intermediate shade tolerant species (Abrams and Kubiske 1990). Northern red oak sprouts tend to be more frequent on smaller stumps, but large diameter stumps are still capable of sprouting (Johnson 1975, Wendel 1975). Boles from stump sprouts are resistant to butt rot and may be equally valuable for timber as seedling origin trees (Walters and Yanwey 1990, Johnson 1994).

Paper birch is a short-lived species that grows quickly in mesic mixed hardwood and conifer forests (Safford et al. 1990). Minnesota represents the southern edge of its range, which extends from Alaska across Canada, through the Great Lakes region, to Maine and the Canadian Maritime provinces. Paper birch is shade intolerant and not as long-lived as red maple or northern red oak (Abrams and Kubiske 1990). Paper birch sprouts abundantly, though sprouts tend to have high rates of mortality during the first few years. Paper birch's sprouting rate decreases more rapidly with age than red maple or northern red oak, but mature trees are still able to sprout (Perala and Alm 1990a). Trees from sprouts mature faster than seedling origin trees, through sprout origin trees may deteriorate earlier (Perala and Alm 1990b).

Site description

This study was conducted on seven sites in north-central Minnesota's northern hardwood forests. As the three study species did not occur together on any of the sites, the five maple/oak sites were located in Pine county and the two paper birch sites were located in Itasca county

(Figure 1). Three maple/oak sites and two paper birch sites had sufficient sprouting stumps for a full sample size at least 125 trees per species. On the two remaining maple/oak sites it was only possible to collect a much smaller sample size (Table 1). These two minor sites, MO4 and MO5, were analyzed using the same methods as the main sites but are discussed separately because the smaller sample size resulted in more variable results.

The overstory composition of the maple/oak sites was 40-60% northern red oak with a mixture of other northern hardwoods, primarily sugar maple (*Acer saccharum* Marsh.) and red maple compromising the remainder of the overstory. The residual overstory on the two birch sites consisted of sugar maple, red maple, basswood (*Tilia americana* L.), paper birch, and balsam fir (*Abies balsamifera* Mill.). Sites had an average residual basal area between 8.3 m^2/ha to 19.5 m^2/ha but were chosen to contain high within-site variability in overstory density (0 m^2/ha to 40 m^2/ha, Table 1).

All sites were harvested 5-8 years before the data were collected. All sites were thinned, with the exception of one birch site (B2), which was strip clearcut in 5.5 m strips. The major species harvested on the maple/oak sites was northern red oak with a significant red maple component and small number of other merchantable northern hardwoods (e.g. sugar maple, basswood, etc.). The dominant harvest species on the paper birch sites was paper birch, but a range of other northern hardwoods and a small number of conifers were also harvested.

All sites were gently sloping with small low-lying wet areas that were excluded from the survey. Soil samples (15 cm X 15 cm X 15 cm) were collected at five random points along random transects in each site. The five samples were pooled and soil texture was determined using an adapted hydrometer method (Grigal 1973). Soil analyses showed that all the sites were Sandy Loams (see Table 1). The soils in all the sites was comprised of approximately 70% sand,

25% silt, and 5% clay, except for one maple/oak site and one birch site (see Appendix: Table 6). Soils on these two sites (MO2 and B1) had about 50% sand, 45% silt, and 5% clay. The site indices for all sites were between 20 and 25 m (for northern red oak or aspen, DNR & County Foresters, pers. comm.).

Field measurements

All measurements were taken in September and October of 2000. Areas with sprouting stump densities of at least one stump per 10 m^2 and with variable overstory densities were identified. A twenty meter wide transect was run in a straight line through these areas until the transect entered an area with insufficient stump density or reached the edge of the harvest area. To avoid spatial autocorrelation, sprouting stumps less than five meters from already measured stumps were not used. Each sprouting stump encountered on the transect was measured for the following: 1) yearly height growth of tallest sprout for past two years (F1 & F2, cm), 2) height of tallest sprout (HT, cm), 3) diameter at breast height (130 cm) of tallest sprout (D.B.H., mm), 4) average height of all live sprouts (AH, cm), 5) stump diameter (SD, cm), 6) total number of living stems, browsed and unbrowsed (STEMS), 7) number of times the apical bud on the tallest sprout was browsed (APICAL), and 9) basal area of overstory trees around the stump (BA, m^2/ha). Any stump with all sprouts browsed below the one and a half meter mark (i.e. completely browsed) was not used.

HT and AH were measured with a height pole. AH was measured by taking a reading off the height pole when the tip of the pole was estimated to be at the average height of the live sprouts (browsed and unbrowsed). DBH was measured with an analog caliper at breast height. SD was the average of the two largest perpendicular measurements of stump diameter. STEMS was the count of all living sprouts (browsed and unbrowsed) on the stump. APICAL was the

number of times the dominance in the tallest sprout changed from the apical leader to a lateral leader; it was considered an estimate of the number of times that sprout had been browsed. BA was measured with a 2-factor prism from the center of the sample stump. All live trees were tallied by species, while snags were noted separately.

F1 and F2 were the distance between the overwintering bud scars on the tallest sprout on a given stump. Determining bud scars was straightforward for birch and maple since they only have one flush per year. Determining the yearly growth in northern red oak was more complicated since it may flush multiple times, leaving more than one bud scar per year. However, overwintering bud scars on oak sprouts had an associated color change in the stem, making determination of yearly growth unambiguous. After examining a large sample of birch stump sprouts in the field, it was found that bud scars from the previous year could not be clearly determined, so previous year's growth (F2) was not reported for birch. Flush measures were not taken for any sprout if the yearly growth had been visibly damaged.

Data Analysis

Standardization methods

To compensate for unequal site conditions (Table 2, Appendix: Table 1) and a different age of the sprouts, all dependent variables were standardized. Each dependent variable was divided by the average value of all the unbrowsed sprouts in the lowest 5 m^2/ha overstory of basal area (i.e. sprouts in the most favorable growing conditions for the site). All analyses were performed on the relativized measures. Relativized variables are denoted with a "Rel" prefix.

To compare the magnitude of the effects between each dependent variable in the model, the value of each linear coefficient was standardized. To standardize the coefficients, each

coefficient was multiplied by the standard deviation of the variables they modified (D. Cook, Univ. of MN Department of Statistics, pers. com.). Overstory density coefficient values could not be compared to other dependent variables using this method since the two non-linear coefficients have no linear equivalents.

Non-linear regression

Non-linear multiple regression models were used to examine the relationship between each relative growth/size measure (RelHT, RelAH, RelDBH, RelF1, RelF2) and the independent variables (BA, APICAL, SD, and STEMS). Plots of the residuals against the predicted values were examined for violations of model distribution assumptions. Regression models were fit using the ARC statistical program (Cook and Weisberg 2000).

To accommodate a non-linear relationship between growth and overstory density, a reverse exponential model fit the relationship between growth or size and residual basal area:

$$\text{RelY} = \alpha_0 * e^{(\alpha_1 * \text{BA})} + \alpha_2 * \text{SD} + \alpha_3 * \text{Apical} + \alpha_4 * \text{Stems} \quad (1)$$

Where RelY is any of the dependent variables, α_x is a coefficient corresponding to the independent variable which follows it. The model has an asymptote at zero and can have either a concave or a convex curve, depending on the sign of α_1. Each species was fit separately and site interactions for each coefficient were added to the model to accommodate differences between the sites. Maple/oak site 5 had extremely low browsing levels so the browsing coefficient was dropped from the model for that site.

The effect of overstory density (BA) consisted of two coefficients. The α_0 coefficient is the predicted value when BA=0 (i.e. the intercept). The value of the intercept (α_0) is a function of the constant used to make the measures relative for each site and by itself is not an instructive

measure of the effect of overstory density on sprout growth and size. The α_1 coefficient controls the slope and therefore defines the change in the growth or size of the sprouts over the range of overstory densities. For the purposes of the analysis, the term "effect of overstory density" will refer to the coefficient α_1 in the results and discussion of this paper.

To test for significant effects of individual variables and interactions, each variable or site by variable interaction was dropped individually and an F-test was used to detect significant changes in the model fit from the loss of the term ($p<0.05$). Non-linear t-tests (Delta-method, Seber and Wild 1989) were used to test differences between oak and maple fits on each site. A standard T-test was used to test for differences between fits for different growth or size measures ($p<0.05$). No statistical tests could be performed comparing paper birch to northern red oak and red maple since they were not collected on the same sites.

To test if browsing was affecting the overall response of sprouts to the other factors in the model, a model with only unbrowsed sprouts was compared to the full model and the coefficients were compared to the coefficients of the full model using a t-test test.

Overstory composition

To test for differences in sprout growth under canopies composed of shade tolerant trees and shade intolerant trees, a modified version of the non-linear model (1) was used:

$$RelY = \alpha_0 * e^{(\alpha_{10} * BA_{SI} + \alpha_{11} * BA_{IN} + \alpha_{12} * BA_{ST})} + \alpha_2 * SD + \alpha_3 * Apical + \alpha_4 * Stems \quad (2)$$

Where BA_{SI} is the total BA of all shade intolerant trees in the BA count for each stump. BA_{IN} and BA_{ST} correspond to the intermediate shade tolerant and shade tolerant trees, respectively. The shade tolerance class for each species was based on Abrams and Kubiske 1990 and Burns and Honkala 1990. The model allowed for an individual α_1 coefficient for each class of shade

tolerance. This forced the effect of all of the shade tolerance classes to be equal when the overstory density (BA) was zero, but allowed each shade tolerance class to an have independent effect on growth over the range overstory density (BA). The linear portion of the model remained unchanged. The model was fit with data from each species and each site individually because of site differences. An F-test was used to test for significant changes in the model fit from splitting BA into three measures. The differences between each BA coefficient was tested with a non-linear t-test (Delta-method, Seber and Wild 1989).

Results

The regression analyses found that all of the species on all the sites had similar patterns of responses of relative growth and size to changes in overstory basal area (BA), browsing (APICAL), total number of stems (STEMS), and stump diameter (SD). Models using the five different relative growth and size measures had large differences in their goodness of fit. The models for relative height (RelHT), relative average height (RelAH), and relative diameter (RelDBH) all had a better fit than either annual growth measure (F1 and F2; $r^2 \approx 0.5$ vs. $r^2 \approx 0.2$, Table 3). The analyses that follow, therefore, focus on the three main relative size measures; relative height, relative average height, and relative diameter. The two relative growth measures, RelF1 and RelF2, are discussed when their regressions differed substantially from the other three.

Standardizing the size and growth measures removed many, but not all, of the differences between the sites. All of the sites had the same basic relationship between the variables measured, but the effect of site could not be removed from the models for northern red oak and red maple stumps ($p<0.001$, F-test.). The final model for northern red oak and red maple contained site interactions for both coefficients of BA (α_0 only for site 1, α_1 for all three sites), and STEMS. There was no effect of site on paper birch sprout size ($p=0.11$, F-test); therefore, site was dropped for paper birch in the final model.

Overstory density

In general, as overstory density increased, sprout sizes decreased on the three main sites ($p<0.05$, Figure 2 & Table 2). The only two exceptions to this effect occurred in northern red oak sprouts when using the relative average height of all sprouts as the size indicator. In both

cases, the effect of overstory density was not significantly different than zero ($p>0.1$, Site MO2 and MO3). For red maple and paper birch, the effect of overstory density was significant for all sites and size measures.

The exponential curve in the non-linear model was not pronounced for many of the fits, especially for northern red oak, but there was a clear negative relationship between overstory density and the size measures (Figures 2 & 3). Increasing overstory density tended to reduce red maple sprout size more than it reduced northern red oak sprout size (Figure 2) though red maple sprouts were taller and had larger diameters, on average, on all sites (Table 2). This difference between red maple and northern red oak sprouts was significant on Site MO2 for all size measures ($p<0.01$). It was also significant on Site MO1, but only for diameter of the tallest sprout ($p=0.05$). There was no significant difference between the growth response of red maple and northern red oak sprouts on Site 3. The effect of overstory density on paper birch sprouts was intermediate between northern red oak and red maple (Figure 3).

The effect of overstory density on sprout size was different between the three main sites ($p<0.001$), though the basic relationship was consistent across three sites (Figure 2). The percent reduction in stump sprout size from an open canopy (0 m^2/ha) to a closed canopy (30 m^2/ha) was similar for all three species on all three main sites (Tables 4 & 5). Maple/oak site 4, a minor site, did not have a significant effect of overstory density on relative height, relative average height, or relative diameter for northern red oak or red maple (Appendix: Table 3). Graphs of the data from site 4 (not shown) suggested that this was because of a limited sample size. The effect of overstory density on Maple/oak site 5, which had only red maple sprouts, was very similar to the effect of overstory density on the three major sites (Appendix: Table 3).

Though, snags were measured separately and not included in the BA count for the models, they made up only a small fraction of the BA count on all of the sites. Adding the BA of the snags into the total BA in the model did not significantly change the model fit for any species ($p>0.05$).

Browsing

Browsing of the tallest sprout had a negative impact on sprout size for all sites and species ($p<0.001$). The minor site, Maple/oak 4, had very similar effects of browsing on relative height, relative average height, and relative diameter. For all species, increased browsing on the tallest sprout resulted in decreased size. The effects of browsing varied little between northern red oak and red maple or between size measures (Figure 4). In paper birch, browsing had more of an effect on relative height of the tallest sprout and relative average height of all sprouts than on relative diameter of the tallest sprout ($p<0.02$).

Fitting the model with only unbrowsed sprouts resulted in no large differences between any of the coefficients for overstory density, stump diameter or stems ($p>0.05$, data not shown) indicating that browsing did not interact with other factors in the model (i.e. the effect of overstory density on northern red oak was not effected by browsing).

Stump Diameter

Stump diameter did not always have a significant effect on sprout size. On the main sites, as red maple stump diameter increased, sprout size increased ($p<0.001$, Fig. 5). Stump diameter had no effect on northern red oak or paper birch sprouts ($p>0.05$) in all cases but relative average height of northern red oak sprouts ($p=0.03$). The effect of stump diameter on sprout size in red maple was significantly greater than in northern red oak or paper birch

($p<0.02$). Red maple stumps on the study sites were significantly smaller than northern red oak or paper birch stumps ($p<0.001$). The two minor sites also had a small effect of stump diameter on sprout size, but the effect was positive for northern red oak and red maple. In some cases the effect was non-significant ($p>0.1$).

Stems

There was no significant effect of total stems on sprout size for northern red oak or paper birch on the main sites ($p>0.1$), except relative diameter of the tallest stem and height of the tallest stem on the MO3 site. In most cases, there was also no significant effect of stems on sprout size for red maple ($p>0.05$). The exceptions were relative height of the tallest stem on sites MO1 and MO3 and relative diameter of the tallest stem on Site MO3. On the two minor sites, there was no significant effect of the total number of stems on sprout size for red maple ($p>0.1$) but northern red oak sprout size (for all measures) had a significant increase with increasing sprout numbers ($p<0.02$). However, the overall effect of number of stems on sprout size in northern red oak, though significant, was small.

Comparisons between factors

Browsing and overstory density had larger effects on relative sprout size than stump diameter and total stems. Using the standard deviation standardization for each coefficient (see methods), a comparison of the linear variables (browsing, stump diameter, total stems) found that the largest effect on sprout size was browsing. In red maple, the effect of the browsing coefficient was, on average, 1.4 times larger than the effect of coefficient for stump diameter (Appendix: Table 4). The difference between the effects of browsing and total stems was even larger (average of 11.5 times greater, Appendix: Table 4). Northern red oak and paper birch also

followed this pattern (Appendix: Table 4). Because there was a great variability in the coefficients, there was also great variability in the differences between the coefficients. In all cases, however, the adjusted browsing coefficient was larger than the corresponding adjusted total stems or stump diameter coefficient (i.e. the values in Appendix: Table 4 are all greater than 1).

Though the non-linear overstory density coefficients could not be compared directly with linear variables, graphs of the non-linear equations show that the magnitude of the effect of BA is equal to or larger than the effect of browsing across the respective ranges of overstory density (Fig. 2 & 4). The main effects, therefore, on the size and growth of sprouts were overstory density and browsing. Stump diameter and total stems had minor, but significant effects.

Differences between growth and size measures

All of the growth and size measures had similar responses in the regressions, but there were notable differences. For red maple and northern red oak, the three size measures (RelHT, RelAH, RelDBH) had similar goodness of fits ($0.49 < r^2 < 0.54$ for red maple, $0.46 < r^2 < 0.47$ for northern red oak, Table 3). The models using the size measures had higher goodness of fits than the models using the growth measures (F1, F2). Paper birch models had much poorer goodness of fit values than northern red oak or red maple models (e.g., 0.51 vs. 0.15 for RelDBH in red maple vs. paper birch, Table 3).

Since all of the growth and size measures were standardized and had similar standard deviations, comparisons between the values can be made. In red maple, the largest difference between the fits of the size measures was that the α_1 term (i.e. the effect of overstory density, Equation 1) was significantly larger for relative diameter then for relative height or relative average height ($p < 0.04$). Northern red oak followed this pattern but the differences were only

significant in some cases (RelAH; MO2: p=0.04, MO3: p=0.003, RelHT; site 3, p=0.02). Paper birch also followed this pattern (RelHT; p=0.05, RelAH; p=0.09). This indicates that for all three species, but most prominently in red maple, relative diameter is more sensitive to overstory density than relative height or relative average height.

Red maple stump sprout relative diameter increased more as a result of higher stump diameter than relative height or relative average height ($p < 0.006$), but northern red oak and paper birch did not ($p>0.2$, Figure 5). For paper birch, browsing had a smaller effect on relative diameter than on relative height or relative average height (p=0.02). Northern red oak and red maple did not follow this pattern.

Shade Tolerance Effects

There was no significant difference between the effect of each shade tolerance class on growth or size ($p>0.05$) for any site or species (data not shown). It is important to note, however, that none of the sites had even distributions of shade tolerance classes in the canopy. The three maple/oak sites had similar overstory composition as did the two paper birch sites, but there were large differences between the two groups (Appendix: Table 2). The maple/oak sites were dominated by northern red oak, i.e., the canopy was largely made up of intermediate shade tolerant trees. Shade tolerant trees dominated the canopy of the birch site 1 whereas the canopy of birch site two was dominated by shade intolerant trees, mostly paper birch.

Site Differences

Though all values were standardized to attempt to compensate for site differences, there were still significant differences between the sites. Significant site interactions were found only in red maple and northern red oak, and in those two species, only with overstory density and total

stems. Most of the individual overstory density and site interactions were non-significant, but their overall effect on the model was significant ($p > 0.05$). In one case only, sites MO2 vs. MO1, red maple sprouts showed a significantly smaller effect of overstory density on the relative average height of all sprouts (Site 3 smaller, $p=0.03$). Red maple sprouts on site 3 had a smaller response overstory density on than sites 1 and 2 for relative height and relative diameter, though the difference was non-significant ($p>0.07$). Northern red oak sprouts tended to have a smaller response overstory density on site 2, but the difference was not significant for relative height, relative average height, or relative diameter ($p>0.05$).

These differences were associated with site characteristics, but the trends were different for red maple and northern red oak. Sprouts on site 3, the significantly different site for red maple, were one year younger the sprouts on other two sites (Table 1). Soils on site 2, the site that was different for northern red oak, had higher silt content and one more year of growth (Table 1 and 6). The overstory species composition did not appear to be associated with the differences in time since harvest and in soils between the sites. The largest differences in canopy species composition were between the two birch sites, which were the two sites with no site interaction.

Discussion

General sprout responses

In general, sprouts of all three species on all sites responded similarly to overstory density, browsing, and stump diameter. I will first discuss the overall patterns found for all species across the sites and follow this discussion with an examination of the differences that were found between the species and between the sites.

Increasing overstory density significantly reduced sprout size (relative height, relative diameter, and relative average height) in red maple, northern red oak, and paper birch in all but two models on the main sites. The two minor sites (sites 4 & 5) showed the same effect of overstory density on sprout size though in many cases the effect was not significantly different than zero because of the smaller sample size (Table 1). Other studies found a similar effect of overstory on stump sprouting. The other studies which measured stump sprouting under differing overstory densities (Comeau et al. 1998, Gardiner and Helmig 1997) found that increasing overstory density resulted in larger reductions in sprout height per m^2/ha of overstory than my study (e.g. 49% reduction in paper birch in Comeau et al. 1998 compared to 29% in my study). Studies on seedling response to overstory have also found similar responses (Finzi and Canham 2000, Pacala et al. 1994). The larger reductions found in other studies may have been because differences in site quality or in species sensitivity to conditions altered by the overstory. Sprout diameter growth of all three species tended to be more effected by overstory density than height growth. This pattern has also been found in water oak stump sprouts (Gardiner and Helmig 1997).

This study may have been able to create a clearer picture of the effect of overstory if a direct measure of light (e.g. % transmission) or canopy openness (e.g. overstory cover, gap light index, etc.) had been taken along with the basal area measurement. Basal area and light levels are correlated but the exact light levels under a given basal area depend on species composition (Canham et al. 1994) and crown condition. Though the number of snags and the species composition of the canopy did not appear to affect the model significantly, combining this overstory information with basal area to interpret understory growth conditions added variability to the data.

Browsing reduced the relative height and relative diameter of the tallest sprout. This is not surprising considering that the browsing measure was determined by the number of times the dominance in the tallest sprout changed from the apical leader to a lateral leader. This finding indicates that compensatory growth in stump sprouts is not sufficient to overcome the losses from browsing. The browsing measure used, however, was not an entirely accurate one. Estimating past browsing from the present condition of the sprout, the measure used by my study, may have overlooked browsing events and may have included other, non-browsing events which had similar effects on the tallest sprout (i.e. loss of apical dominance). A direct measure of browsing (e.g. herbivore exclusion) or artificial browsing would have solved many of these difficulties.

Stump diameter did not have a significant effect on stump sprout size or growth for northern red oak and paper birch. Other studies found that the effect of stump diameter varies with the species and relative diameter ranges measured (Mroz et al. 1985, Harrington 1984, Lynch and Bassett 1987). The relationship between red maple sprouts and stump diameter in my study was very similar to the relationship found by Mroz et al. (1985) for red maple. However, the diameter range of my study did not include the larger diameters in which Mroz et al. (1985) found a plateau where increased stump diameter no longer resulted in increased sprout growth.

While my study shows that stump diameter does not have a large effect on the size of stump sprouts, it should not be construed that stump diameter, and by association, stand age is not a large determinant of the regeneration from stump sprouting in a stand after harvest or disturbance. Stumps that failed to sprout after harvest were not measured and the transect locations were chosen to contain a high density of sprouting stumps, which biased the results. Older stands may have had very low sprouting probability and minimal regeneration from stump

sprouts. I found healthy sprouts on stumps over 40 cm for red maple and 60 cm for paper birch and northern red oak. I did not find that larger stumps had smaller sprouts, which indicates that even if larger stumps have lower sprouting probability, they can still produce equally vigorous sprouts. Moreover, for red maple, it appears that larger stumps, when they do sprout, produce marginally more vigorous sprouts.

Species Differences

Red maple, though classified as shade tolerant, grows rapidly in all conditions (Abrams 1998), and thus appears to be an exception to Reich et al's (1998) generalization that shade intolerant seedlings grow better than shade tolerant species in low and high light. Northern red oak seedlings, due to a high proportion of resource allocation to roots, tends to grow slowly under all light conditions despite being classified as moderately shade tolerant (Walters and Reich 1996).

My study supports many of the previous findings on seedlings (e.g. Walters and Reich 1996, Reich et al. 1998), though red maple appears to have characteristics of a shade intolerant tree in terms of growth under open canopy conditions. Overstory canopy density had a significantly larger effect on red maple sprout growth than on northern red oak sprout growth, but the absolute size of red maple sprouts was larger under all canopy conditions on all sites. Though northern oak had higher rates of browsing on all sites (Table 2) the unbrowsed northern red oak seedlings, when considered separately, still had lower growth rates under all conditions, indicating that browsing was not the sole cause of smaller northern red oak sprouts.

The two paper birch sites differed in site quality and browse levels, making it difficult to compare the absolute size measures with red maple and northern red oak. It is also impossible to distinguish site differences from species differences in paper birch since it was collected on a

different site. It is still noteworthy, however, that effect of overstory on birch sprout growth was closer to red maple than to northern red oak (Tables 4 & 5). Reich et al. (1998) used paper birch as a shade intolerant species and found that paper birch germinants grew better than shade tolerant species under high and low light conditions.

There are many possible explanations for why red maple, despite being more shade tolerant, grew better under all overstory densities. The different regeneration strategies between northern red oak and red maple may effect their growth rates under an open versus a closed canopy. Northern red oak seedlings have high levels of root storage (Walters and Reich 1996) and sacrifice above-ground growth to decrease the risk of mortality (Canham et al 1996). If northern red oak stump sprouts maintain the same strategy as seedlings, red maple stump sprouts would be expected to have higher stem growth rates because they would be putting more resources into above ground growth.

Growing conditions on the sites may have been more optimal for red maple than for northern red oak. Northern red oak appears to grow on sandier sites than red maple (Crow et al. 1988, Abrams 1998), but red maple can prosper on very wide range of sites, including sandy soils (Walters and Yawney 1990, Abrams 1998). The largest difference between northern red oak and red maple sprouts was on MO site 2, which was the site with the soil with the smallest sand content. Red maple seedlings are more negatively effected by soil resource limitation than northern red oak (Canham et al. 1996). The sandier sites, where there was less of a difference between northern red oak and red maple, may have afforded red maple less of an advantage over northern red oak.

Another possibility is that sprout origin red maple growth patterns are different than seed origin red maple growth patterns. Red maple was not used as a shade tolerant species in any of

the studies on shade tolerance relationship to high and low light (Walters and Reich 1996, Reich et al. 1998a, Reich et al 1998b, Walters and Reich 2000) but red maple was found to have the largest percent increase in growth from low light (2%) to moderate light (45%) of four species of seedlings (white pine (*Pinus strobus* L.), northern red oak, red maple and sugar maple, Canham et al. 1996). This evidence, and the indication that northern red oak and paper birch followed the same patterns as seedlings, indicates that the hypothesis that red maple sprouts behave differently than seedlings is unlikely.

Other studies that examined the effect of overstory density on sprout growth only looked at single species, making it difficult to compare results in relation to shade tolerance. Of the four species covered in the previous studies, two are shade intolerant (paper birch, Comeau et al. 1998, and water oak, Gardiner and Helmig 1997) and two are shade tolerant (sugar maple, Church 1960, and bigleaf maple, Tappeiner et al. 1996). Both shade tolerant and shade intolerant species showed a significant increase in sprout growth with decreased overstory density. The experimental design and site conditions of the four studies were too dissimilar to make any quantitative comparisons.

While my study cannot rule out any of the hypotheses as to why red maple fit the pattern of a shade intolerant species, it demonstrates that shade tolerance rankings may not be the most effective means to predict regeneration under varying canopy density (Messier et al. 1999). Not only does canopy density affect much more than light availability (Counte 2000), the ability of a species to respond to decreased canopy density may vary according to site conditions (Canham et al. 1996). This is further complicated in stump sprout regeneration because sprouts inherit a root system and carbon stores which may potentially alter stump sprout regeneration dynamics compared to seedlings of the same species.

Site differences

Though each species had a similar response on all the sites measured, there were significant differences between the sites. The differences between the sites for overstory density did not have a clear association with number of growing seasons, soil texture, or overstory species composition. The differences were also not shared between northern red oak and red maple. The red maple site that tended to have the smallest effect of overstory density was the site with the youngest sprouts. The northern red oak site that tended to have the smallest effect of overstory density was site with the oldest sprouts. However, sprouts on all three sites had a year of difference between each of them and there is little reason to suspect that one-year age difference of the sprouts would set that site significantly apart.

There are many factors which were not measured that could have changed the effect of overstory density on the response of the sprouts on each site. The overstory crown architecture, for example, could have had a large effect on understory light conditions (Lieffers et al. 1999) and microenvironment. The number of competing sprouts on each site may have also changed the growing conditions for the tallest sprouts on each stump (Lowell et al. 1989). Site conditions, beyond just soil texture, may have also created differences in the sites. Soil compaction, frost pockets, and stand age could all have changed the growing environment for the sprouting stumps.

The differences between the site interactions with overstory density between red maple and northern red oak indicate that factors that affect red maple may have less of an effect on northern red oak and vice versa. For example, red maple is more sensitive to soil resource depletion than northern red oak (Canham et al. 1996).

Management implications

As forest management of hardwood stands depends more on natural regeneration, stump sprouting will become a larger part of regeneration in northern hardwood forests. The direction of silvicultural development in Minnesota is towards more diverse stands with more residual trees after harvest (Puettmann and Ek 1999). Browsing is also a large factor in determining forest regeneration in Minnesota. In this environment, it is important to develop a better understanding of how stump sprouts regenerate in diverse stands with a residual overstory and heavy browsing.

Though northern red oak appears less sensitive to overstory density, red maple is more vigorous under all canopy conditions. This indicates that where management goals favor northern red oak, other means are required to promote northern red oak sprouts over red maple sprouts. Fire could be an effective tool since it promotes northern red oak seedlings over more shade tolerant competitors (Kruger and Reich 1997) and would be expected to have the same effect on stump sprouts. Additionally, red maple's rise in the landscape has been associated with reduced fire frequencies (Abrams 1998).

My study also demonstrates that sprouting varies across the landscape. To predict sprout growth on each site, a wide range of site conditions must be considered. Canopy conditions and species composition of the overstory can change the understory environment (Canham et al. 1994a, Lieffers et al. 1999) which in turn can effect sprout growth and probability (Johansson 1987, Comeau 1998). Browsing can reduce growth by damaging growing stems or perhaps increase the growth of stump sprouts by accelerating thinning of stump sprouts (Lowell et al. 1989). Site conditions can have an effect on sprout regeneration (Mroz et al. 1985) and can effect species differently (Canham et al. 1996). Harvesting during the growing season can also

negatively effect sprouting probability and growth, especially in younger trees (Kays and Canham 1991).

More research needs to be done on sprouting dynamics, especially regarding overstory density and browsing, to effectively take advantage of the potential contribution of stump sprouts to forest regeneration. With a better understanding of stump sprouting dynamics, stump sprouting has the potential to become a more important part of forest regeneration in northern hardwood forests.

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Table 1. Site characteristics and sample sizes.

Site Code	Growing Seasons (yrs.)	# of Maple Stumps	# of Oak Stumps	# of Birch Stumps	Min-Max BA (m^2/ha)	Texture
MO1	7	111	108		0-40	Sandy Loam
MO2	8	158	123		0-32	S.Loam/Loam
MO3	6	115	141		0-36	S.Loam
B1	6			149	0-28	S.Loam/Loam
B2	5			117	0-26	S.Loam/L.Sand
MO4	6	13	31		12-26	S.Loam/L.Sand
MO5	5	62			2-28	S.Loam/L.Sand

Table 2. Mean values for each site. Units are cm except; Apical(count), Stems (count), DBH (mm) and BA (m^2/ha).

SITE	N	SD	F1	F2	HT	AH	Apical	Stems	DBH	BA
Maple										
All Sites	459	16	54	53	370	264	0.2	10	19	16
MO1	111	17	45	52	330	243	0.3	12	18	12
MO2	158	15	63	55	388	273	0.3	11	19	20
MO3	115	13	49	49	302	192	0.3	8	14	16
MO4	13	12	55	50	271	205	0.4	7	13	18
MO5	62	20	57	61	547	426	0.0	11	34	13
Oak										
All Sites	403	28	43	43	246	181	0.9	10	13	20
MO1	108	31	39	39	214	159	1.2	10	11	21
MO2	123	26	44	45	278	215	1.0	8	14	20
MO3	141	28	41	41	247	168	0.6	9	13	19
MO4	31	35	61	56	263	204	0.8	14	14	19
Birch										
All Sites	266	31	71	N/A	435	339	0.3	13	28	11
Grasslot	149	32	92		625	495	0.0	8	41	8
IT2	117	31	42		251	190	0.5	18	12	13

Table 3: Multiple regression equations for each site, species and size measure*.

RelHT	BA	SD	Apical	Stems	R^2	N
Site 1						
Red Maple	$0.811\ e^{(-0.0127*BA)}$	0.00485	-0.154	0.00688	0.54	111
Red Oak	$0.686\ e^{(-0.0100*BA)}$	0.00109	-0.111	*0.00332*	0.47	108
Site 2						
Red Maple	$0.886\ e^{(-0.0180*BA)}$	0.00485	-0.154	*-0.00022*	0.54	158
Red Oak	$0.885\ e^{(-0.0068*BA)}$	0.00109	-0.111	*0.00541*	0.47	123
Site 3						
Red Maple	$0.886\ e^{(-0.0099*BA)}$	0.00485	-0.154	0.01139	0.54	115
Red Oak	$0.885\ e^{(-0.0134*BA)}$	0.00109	-0.111	0.01181	0.47.	141
Paper Birch	$0.966e^{(-0.0125*BA)}$	*0.00081*	-0.116	*0.00338*	0.16	266

RelAH	BA	SD	Apical	Stems	R^2	N
Site 1						
Red Maple	$0.857\ e^{(-0.0160*BA)}$	0.00620	-0.119	*0.00257*	0.49	111
Red Oak	$0.669\ e^{(-0.0093*BA)}$	0.00212	-0.095	*0.00074*	0.46	108
Site 2						
Red Maple	$0.902\ e^{(-0.0156*BA)}$	0.00620	-0.119	*-0.00303*	0.49	158
Red Oak	$0.877\ e^{(0.0007*BA)}$	0.00212	-0.095	*0.00368*	0.46	123
Site 3						
Red Maple	$0.902\ e^{(-0.0079*BA)}$	0.00620	-0.119	*0.00369*	0.49	115
Red Oak	$0.877\ e^{(-0.0036*BA)}$	0.00212	-0.095	*0.00239*	0.46	141
Paper Birch	$1.014\ e^{(-0.0150*BA)}$	*0.00045*	-0.135	*-0.00012*	0.21	266

RelDBH	BA	SD	Apical	Stems	R^2	N
Site 1						
Red Maple	$0.756\ e^{(-0.0330*BA)}$	0.01130	-0.176	*0.00322*	0.51	108
Red Oak	$0.606\ e^{(-0.0180*BA)}$	0.00146	-0.158	*0.00252*	0.46	104
Site 2						
Red Maple	$0.828\ e^{(-0.0289*BA)}$	0.01130	-0.176	*-0.00110*	0.51	128
Red Oak	$0.952\ e^{(-0.0099*BA)}$	0.00146	-0.158	*0.00776*	0.46	122
Site 3						
Red Maple	$0.828\ e^{(-0.0266*BA)}$	0.01130	-0.176	0.0156	0.51	115
Red Oak	$0.952\ e^{(-0.0224*BA)}$	0.00146	-0.158	0.0158	0.46	137
Paper Birch	$0.925\ e^{(-0.0230*BA)}$	*0.00368*	-0.136	*0.00088*	0.14	265

*Each site and species is listed individually, though the regressions performed with all sites in one model (but with separate regression for each species). BA coefficients listed as they appear in Equation 1 (e.g. $\alpha_0\ e^{(\alpha_1 * BA)}$). Coefficients in italics were non-significant ($p<0.05$).

Table 4. Percent reduction in relative height of the tallest sprout from open canopy (0 m^2/ha BA) to closed canopy (30 m^2/ha) predicted by regression models.

	RelHT		
Species	Site 1	Site 2	Site 3
Red Maple	28	40	23
Red Oak	27	18	29
Paper Birch*		30	

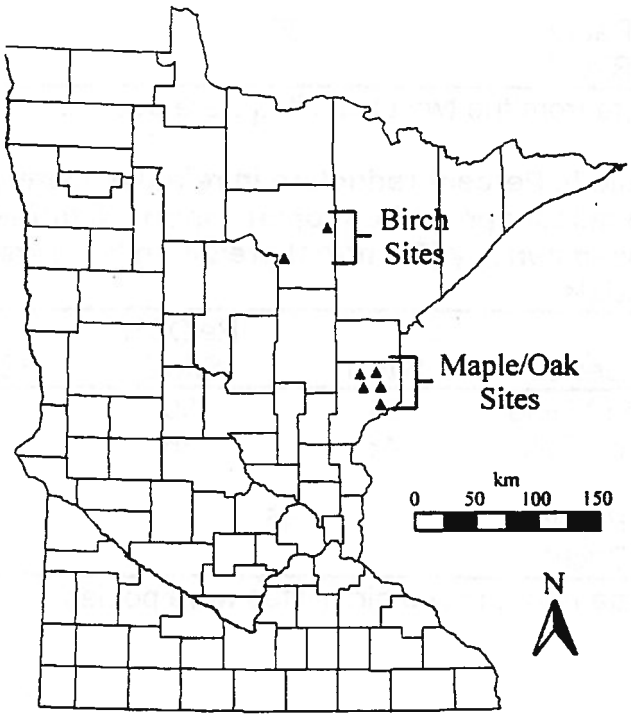
*Data from the two birch sites were pooled.

Table 5. Percent reduction in relative diameter of the tallest sprout from open canopy (0 m^2/ha BA) to closed canopy (30 m^2/ha) predicted by regression models.

	RelDBH		
Species	Site 1	Site 2	Site 3
Red Maple	51	50	43
Red Oak	45	26	43
Paper Birch*		45	

*Data from the two birch sites were pooled.

Figure 1. Approximate locations of field sites in Minnesota.



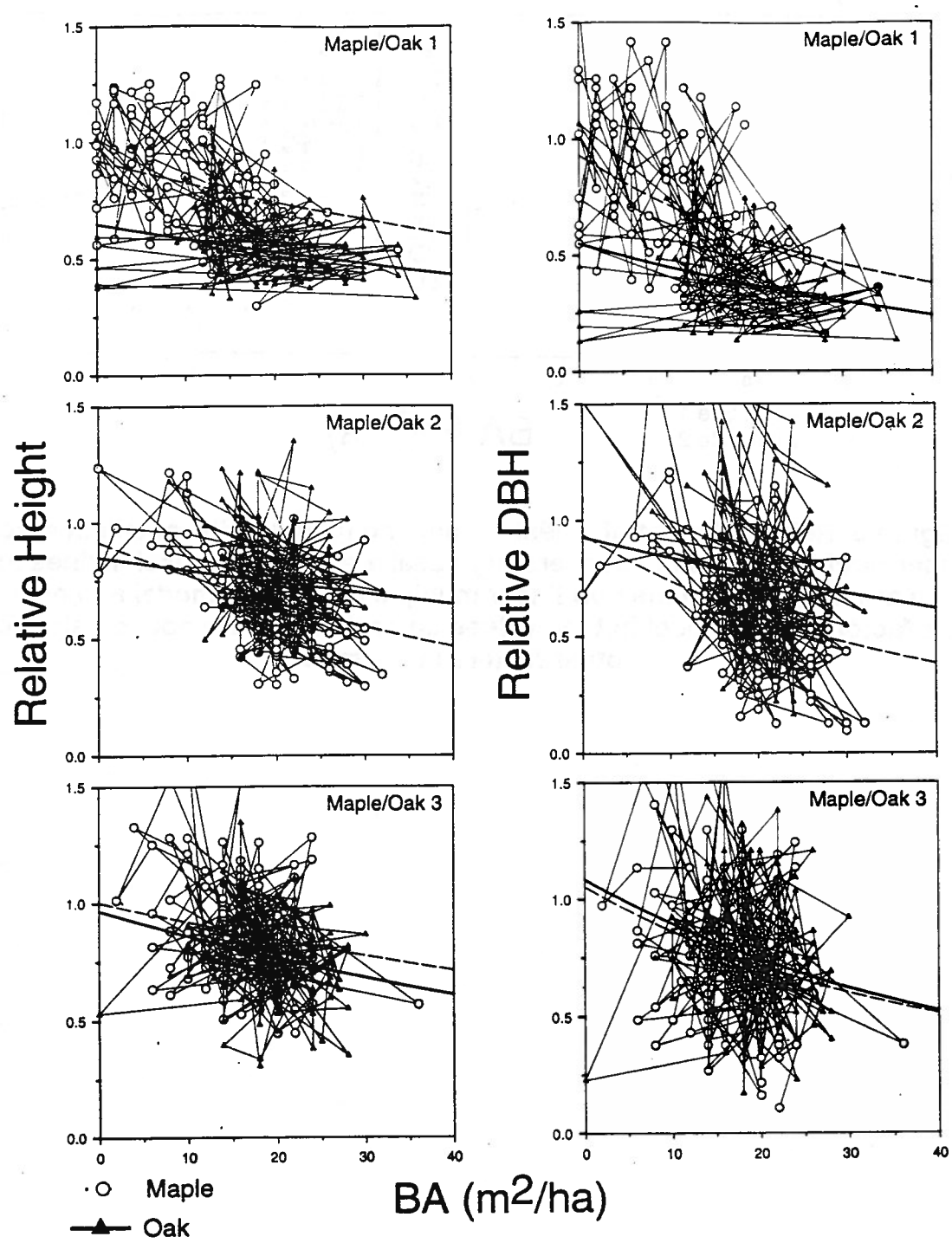


Figure 2. Relative height of tallest sprout and relative DBH of tallest sprout of red maple and northern red oak as a function of overstory basal area. Each species and site is plotted individually. The regression lines in each graph are derived from the non-linear multiple regression model and reflect all of the factors in the model but the values on each graph are not adjusted for the other factors in the model.

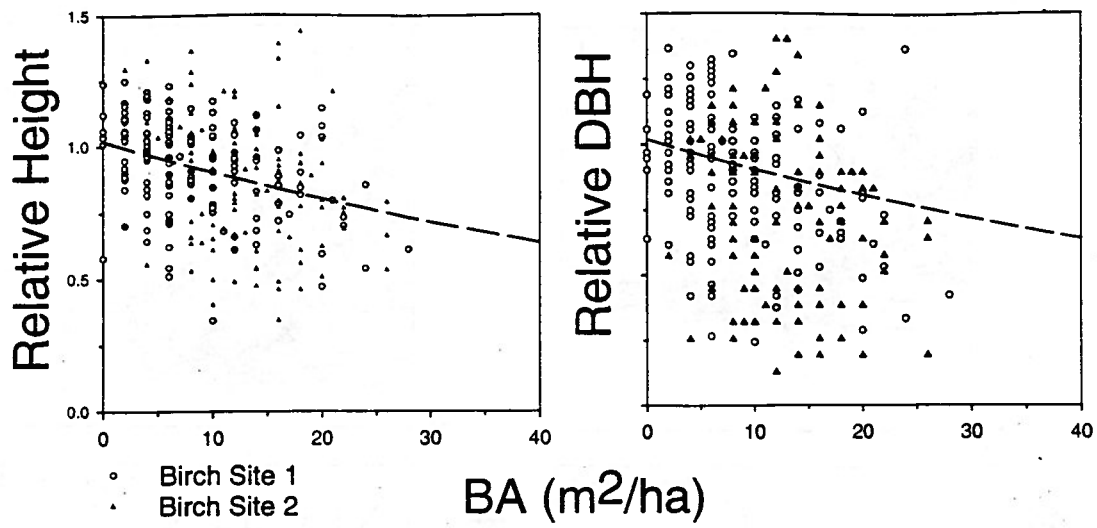


Figure 3. Relative height of tallest sprout and relative DBH of tallest sprout of paper birch as a function of overstory basal area. The regression lines in each graph are derived from the non-linear multiple regression model and reflect all of the factors in the model but the values on each graph are not adjusted for the other factors in the model.

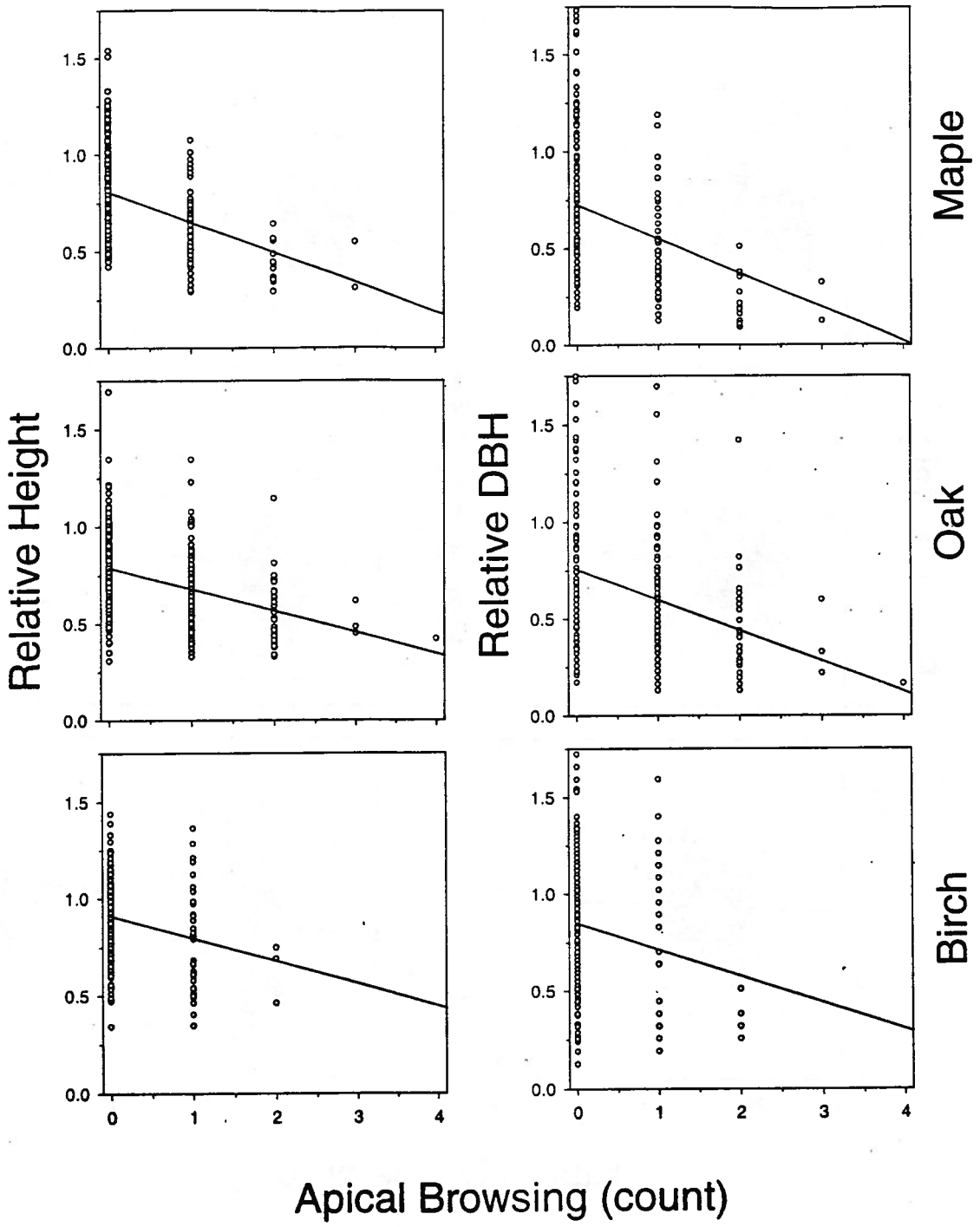


Figure 4. Relative height of tallest sprout and relative DBH of tallest sprout as a function of apical browsing events. The regression lines in each graph are derived from the non-linear multiple regression model and reflect all of the factors in the model but the values on each graph are not adjusted for the other factors in the model.

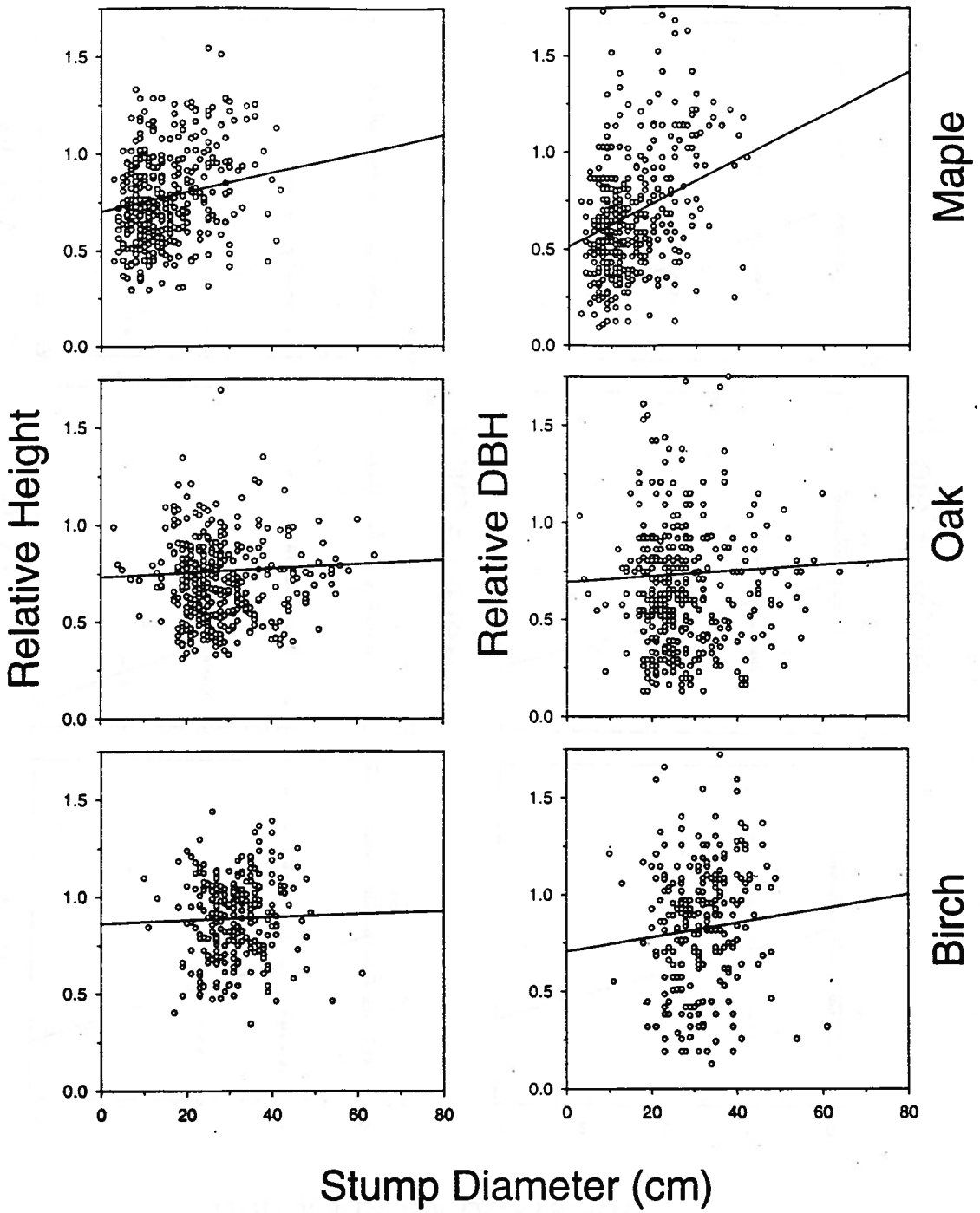


Figure 5. Relative height of tallest sprout and relative DBH of tallest sprout as a function of stump diameter. The regression lines in each graph are derived from the non-linear multiple regression model and reflect all of the factors in the model but the values on each graph are not adjusted for the other factors in the model.

Appendix.

Table 1. Soil Texture by Site.

Site	%Sand	%Clay	%Silt	Texture
B1	46	7	47	S.Loam/Loam
MO2	49	6	45	S.Loam/Loam
MO1	66	3	31	S.Loam
MO3	68	6	27	S.Loam
B2	72	10	18	S.Loam/L.Sand
MO4	76	6	19	S.Loam/L.Sand
MO5	76	7	18	S.Loam/L.Sand

Table 2. Proportion of trees in each shade tolerance class. ST=Shade Tolerant, IT=Intermediate Shade Tolerant, SI=Shade Intolerant

	ST	IT	SI
M01	22	73	4
M02	5	92	2
M03	19	80	1
M04	27	72	1
M05	7	88	5
B1	82	11	8
B2	34	0	66

Table 3: Multiple regression equations for each minor site, species and size measure*.

RelHT	BA	SD	Apical	Stems	R^2	N
Site 4						
Red Maple	$0.748\ e^{(0.0079*BA)}$	*0.0090*	-0.159	*0.00270*	0.43	13
Red Oak	$0.829\ e^{(-0.0052*BA)}$	0.00463	-0.173	0.00857	0.63	26
Site 5						
Red Maple	$0.843\ e^{(-0.0170*BA)}$	0.00547	N/A	*-0.00371*	0.28	62

RelAH	BA	SD	Apical	Stems	R^2	N
Site 4						
Red Maple	$0.731\ e^{(0.0123*BA)}$	*0.0175*	-0.194	*-0.0174*	0.50	13
Red Oak	$0.838\ e^{(0.0018*BA)}$	0.0048	-0.142	0.0056	0.51	26
Site 5						
Red Maple	$0.783\ e^{(-0.0062*BA)}$	0.0077	N/A	*0.00379*	0.13	62

RelDBH	BA	SD	Apical	Stems	R^2	N
Site 4						
Red Maple	$0.772\ e^{(-0.0155*BA)}$	0.0199	-0.268	*-0.02941*	0.59	13
Red Oak	$0.754\ e^{(-0.0283*BA)}$	0.0116	-0.237	0.01770	0.59	26
Site 5						
Red Maple	$0.884\ e^{(-0.0354*BA)}$	0.0089	N/A	*-0.00098*	0.28	62

*Each site and species was fit individually. BA coefficients listed as they appear in Equation 1 (e.g. $\alpha_0\ e^{(\alpha_1 * BA)}$). Coefficients in italics were non-significant ($p<0.05$).